PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
108(3):401–435. 1995.

Lovén's law and adult ray homologies in echinoids, ophiuroids, edrioasteroids, and an ophiocistioid (Echinodermata: Eleutherozoa)

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Abstract.—Lovén's law, which is summarized by an AABAB rule, is found to apply to the structure of *Stromatocystites* and *Astrocystites* (edrioasteroids) and *Gillocystis* (an ophiocistioid) and was previously known in echinoids and in Paleozoic ophiuroids. Chance coincidence and convergent evolution are not likely explanations. Lovén's law is interpreted from edrioasteroids as a manifestation of 2-1-2 symmetry, and in echinoids, ophiuroids and ophiocistioids it is interpreted as a vestige of 2-1-2 symmetry. Thus, Lovén's law is a plesiomorphic character that indicates ray homologies. Roman numerals as used by Lovén for echinoids are applied to edrioasteroids, ophiuroids and ophiocistioids. The anterior ray in exocyclic echinoids is ray III, whereas it is ray II in edrioasteroids. This is reconciled by noting that ray II was anterior in the elongate tests of the Ordovician echinoids *Ectinechinus* and *Eothuria.* In echinoids the anterior-posterior axis of the bilateral larva lines up with ray II in the imago [von Übisch's axis of primordial symmetry]. This relation is used to deduce that the anterior-posterior axis of edrioasteroids coincided with the axis of their larvae. Studies by Fell, Strathmann, and Smith are used to speculate that the larval type of Ordovician ophiuroids was a bilateral planktotroph but not yet an ophiopluteus. Lovén's law is a distinctive and fundamental feature of the body plan that validates the Subphylum Eleutherozoa. There are at least two distinct constructions of 2-1-2 symmetry (Eleutherozoa and Blastozoa) and possibly a third (crinoids).

This paper investigates the value of Lovén's law in establishing ray homologies among echinoderms. Lovén's law of heterotropy describes an AABAB pattern of relative sizes of echinoid basicoronal plates. In an earlier paper (Hotchkiss 1978), my a priori hypothesis was that demonstration of the AABAB pattern of Lovén's law in the ambulacra of Paleozoic ophiuroids would establish either the madreporite or the anus as the landmark for homologous orientation of echinoderms. The unexpected finding was that possibly neither the madreporite nor the anus is reliable. Several a posteriori hypotheses came out of that work, including the possibility that Lovén's law may be fundamental to the echinoderm ground plan.

The program for this research was laid out in the earlier paper (Hotchkiss 1978). 1. Attempt to determine which, if any, of the conflicting propositions for designating ray homologies may be the correct proposition. 2. Investigate the location of the plane of hydrocoele closure and the orientation of the embryological or developmental axes as part of this analysis. 3. Attempt to decide whether Lovén's law independently evolved in echinoids and ophiuroids, or whether it is indicative of a recent common ancestry between echinoids and ophiuroids [review also the embryological evidence], or whether it is fundamental to the ground plan of the phylum. 4. Investigate whether Lovén's law is expressed in other echinoderm groups

Table 1.—Quick reference list of the numbered hypotheses (see text).

H0	The null hypothesis that the arrangement of ambulacrals in the different rays is a matter of chance
H1	The hypothesis of a selective advantage that led to convergent evolution of Lovén's law in separate classes of echinoderms
H2	The hypothesis that in edrioasteroids Lovén's law is a manifestation of 2-1-2 symmetry and that in descendent groups it is a vestige of this ancient symmetry [symplesiomorphy]
H3	The hypothesis that ray II was the original anterior ray
H4	The hypothesis that the relation of the anteroposterior axis of the larva to the rays of the imago has remained the same in echinoids, ophiuroids, edrioasteroids, and ophiocistioids
H5	The hypothesis that Lovén's law is fundamental to the ground plan of the clade Eleutherozoa
H6	The hypothesis that there are at least two distinct constructions of 2-1-2 symmetry, that seen in Blastozoa and that in Eleutherozoa

with alternating ambulacral plates (specific example: *Astrocystites*). 5. Attempt to determine the functional significance, if any, of Lovén's law [Jackson (1927) noted that Lovén's law itself is without obvious meaning]. 6. Investigate whether the fidelity of Lovén's law in Paleozoic ophiuroids varies between taxa (not studied). 7. Investigate whether the madreporite has a constant or statistically preferential position with respect to Lovén's law in ophiuroids.

The sequence and progress of the research depended on serendipity. From 1978 to 1992 I accumulated information on bilaterality in echinoderms [e.g., axes of symmetry, situs inversus, teratology, and behavior] but did not gain any new insight into ray homologies. In 1988 I worked out new methods for investigating the location of the madreporite in Paleozoic ophiuroids (point 7 supra). The chance discovery came in 1992 when I noticed an instance of Lovén's law in Smith's (1985) drawing of *Stromatocystites walcotti.* I proposed a new table of ray homologies for edrioasteroids, ophiuroids and echinoids at the second North American Friends of Echinoderms conference and workshop in July 1992 (no published proceedings). The results were confirmed and extended in 1994 when I noticed the instance of Lovén's law in Jell's (1983) drawing of the ophiocistioid *Gillocystis.* Building on previous studies (Hotchkiss & Seegers 1976, Hotchkiss 1979) the new results are used to suggest ray homologies for asteroids. This paper is the first publication of this research. To keep the presentation as direct as possible, complex supporting information is given in numbered notes. Table 1 lists the numbered hypotheses for quick reference.

In this paper, ray identifications that are based on Lovén's law are labeled with Roman numerals [see Note 1]. The labeling that results for edrioasteroids is different from that of Bather (1914a), Regnéll (1966) and Bell (1976a): the anterior unpaired ray is ray II in my labeling, whereas it is ray III in their ray labeling. In Appendix 1 the madreporite of Paleozoic ophiuroids is shown to be located adjacent to ray IV in interradius III/IV.

Lovén's Law in Echinoderms

An essential part of the program for this research was to investigate whether Lovén's law is expressed in other echinoderm groups with alternating ambulacral plates (point 4 supra). Lovén's law is an empirical statement of the unequal sizes of echinoid basicoronal plates (Fig. 1). The five plates that begin the ambulacral columns Ia, IIa, IIIb, IVa, Vb are larger than the basicoronal plates that begin columns Ib, IIb, IIIa, IVb, Va (Lovén 1874, Melville & Durham 1966:fig.

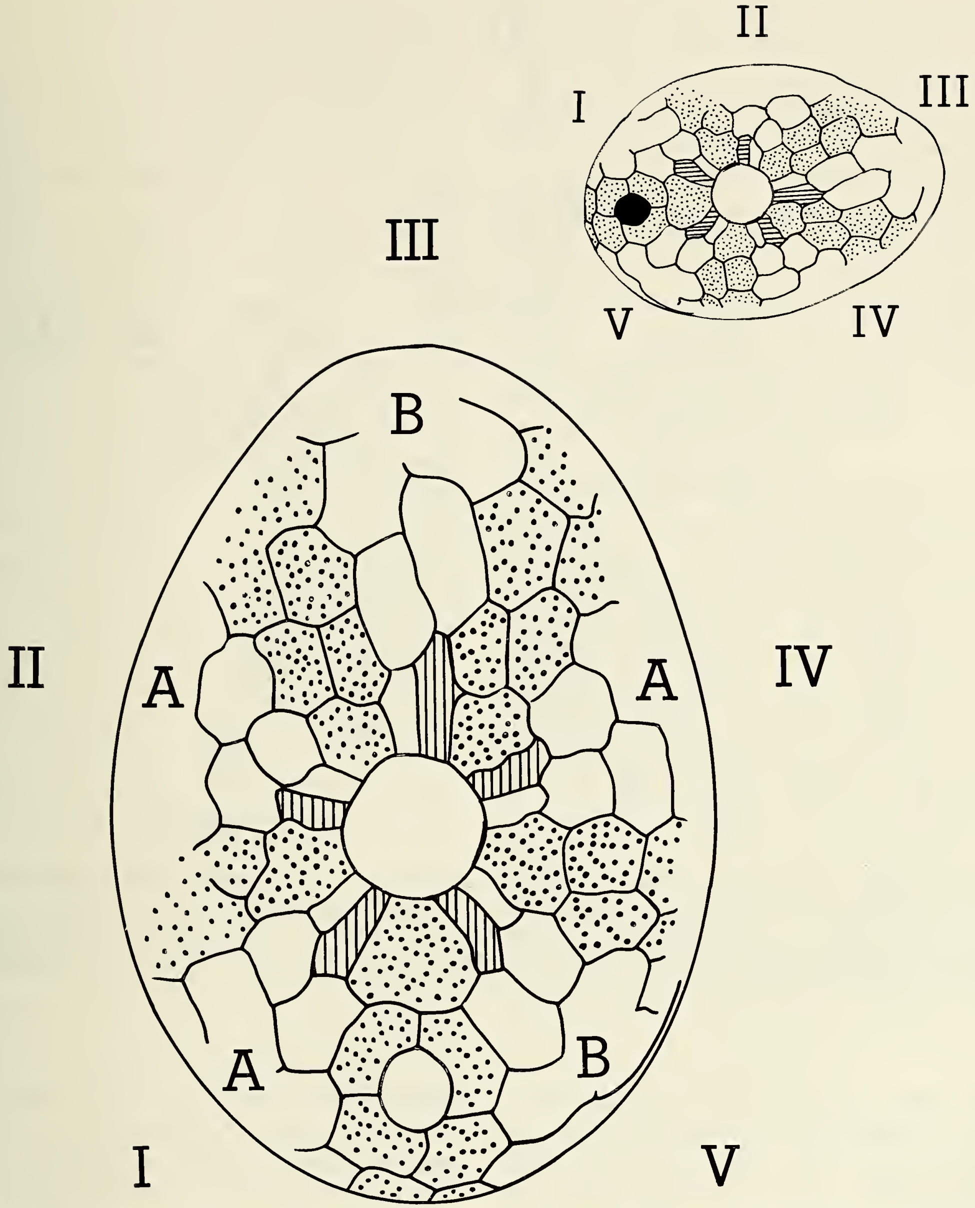

Fig. 1. Lovén's law in the Recent echinoid *Echinocyamus bisexus* (oral side). Basicoronal plates Ia, IIa, IIIb, IVa and Vb, shown vertically ruled, are larger than the unshaded partner basicoronal plates of the same ambulacral area. Interambulacral areas are stippled. Interambulacrum V/I contains the periproct (shown). The madrepore is on the apical surface (not shown); in regular echinoids the madreporic plate is formed by genital 2 in interambulacrum II/III. Although irregular echinoids such as *Echinocyamus* are elongate with ray III anterior, ray II is inferred to have been the original anterior ray in early Paleozoic echinoids and edrioasteroids. In the small insert the echinoid is rotated to have the same orientation as in Figs. 2-5. (Redrawn and annotated from Kier 1968.)

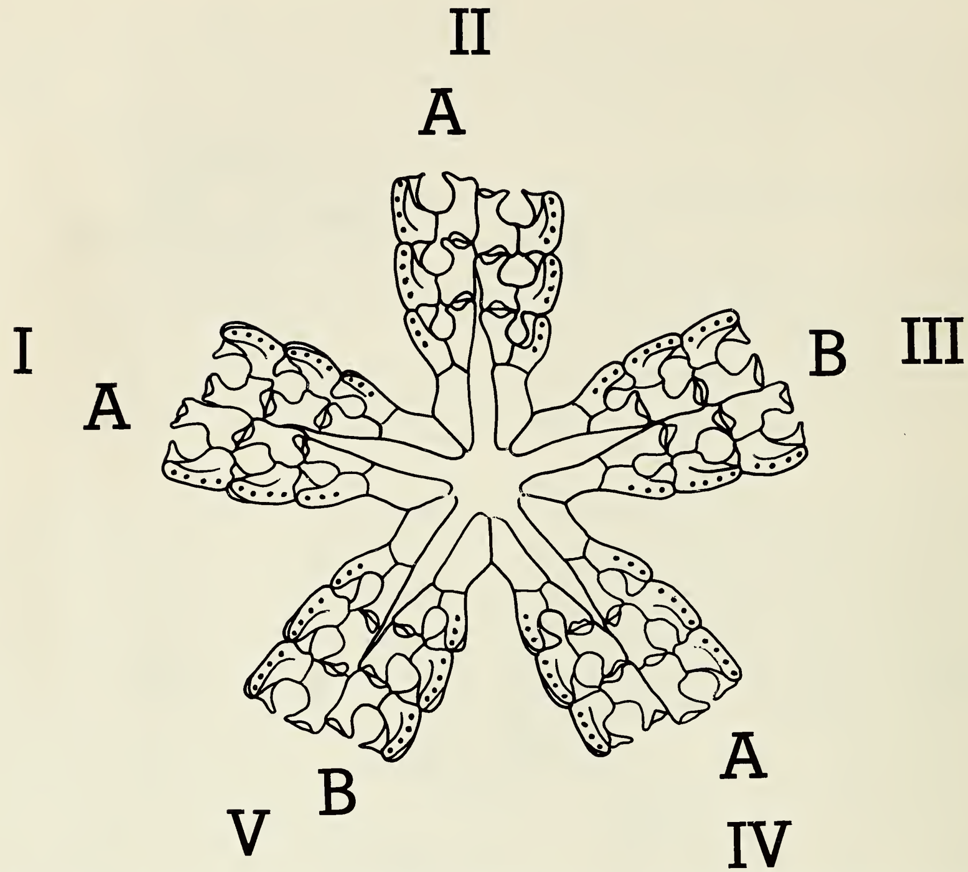

Fig. 2. Lovén's law in the Devonian ophiuroid *Eugasterella thorni* (oral side). The ambulacral half-series on the anticlockwise side of each arm is labeled as either in advance (A) or behind (B) the half-series on the clockwise side of the arm. The arrangement AABAB is Lovénian. From comparisons with edrioasteroids (Figs. 3, 4), ray II is anterior and interray IV/V is posterior. Right posterior interray III/IV contains the madreporite (not shown). (Modified from Hotchkiss 1978; after Kesling 1969.)

164). This arrangement is termed Lovén's law of heterotropy by Gordon (1929) and simply Lovén's law by Melville & Durham (1966:U222). The unequal size of the basicoronal plates initiates columns of echinoid ambulacral plates that alternate according to an AABAB rule (Appendix 1). Based on this rule I showed that Lovén's law applies to Paleozoic ophiuroids that have alternating ambulacral plates (Hotchkiss 1978). Here I report Lovén's law in two edrioasteroids and an ophiocistioid. It could affect the inclusion of somasteroids and asteroids in the clade Eleutherozoa if there was cause to think that they obeyed a law that was different from Lovén's law, or cause to think that they could not obey Lovén's law. I report that somasteroids and asteroids had alternating ambulacral plates (primitive character state) and that it is plausible that Lovén's law will eventually be found to apply to somasteroids and to asteroids.

Echinoids (Fig. 1).—Lovén's law has been so singularly associated with echinoids that it was used by Jackson (1929:508) as part of the evidence that *Bothriocidaris* is properly assigned to the Echinoidea. Lovén's law was found to apply to *Bothriocidaris ar-*

chaica by Jackson (1912:34, 241, plate 1 fig. 1; 1927:451) and to *B. pahleni* by Mortensen (1930) [see also Durham 1966:figs. 214–217]. MacBride & Spencer (1938:121, fig. 10) reported that Lovén's law appears to apply to the Upper Ordovician *Aulechinus grayae.*

Ophiuroids (Fig. 2).—Hotchkiss (1978) reported that Lovén's law applies to Paleozoic ophiuroids and suggested that the ophiuroid madreporite is located in interradius III/IV. Harper (1985) described new material of *Eugasterella logani* (Hall), reporting that it conformed with Lovén's law and that "the madreporite is situated on the disc in interray III/IV, adjacent to the distal portion of the first ambulacral of IV." The association of the madreporite with a ray (now identified as ray IV), as noted by its eccentric location in the interradius, has been documented in both the Zeugophiurina (Sollas & Sollas 1912:216) and the Lysophiurina (Spencer 1914:37, 1925:277, 1934: 459; Hotchkiss 1970:69, Kesling & LeVasseur 1971:329, Petr 1989:8, text-fig. 6). Petr (1989:8, 16) suggested that movement of the lateral plate functioned to uncover and to irrigate the madreporite.

Appendix 1 presents additional data on Lovén's law in Paleozoic Oegophiurida. Complete specimens that obey Lovén's law have the madreporite in interradius III/IV. Analysis of incomplete specimens demonstrates that each arm position relative to the madreporite has a preferred character state, that the preferred character states conform with Lovén's law, and that this pattern identifies the madreporic interradius as III/IV.

Somasteroids.—Lovén's law has not yet been documented in somasteroids. As part of his research on the ancestry of sea stars, Fell (1963a,b,c) studied the morphology of the early Paleozoic somasteroids collected by Thoral (1935) and described by Spencer (1951). He found that the ambulacral ossicles of *Chinianaster* and *Villebrunaster* form opposite pairs in the middle and base of the arm but form alternating series in young specimens and at the tip of the arm in older specimens (1963c:465, fig. 5).

The somasteroid *Archegonaster* has alternating ambulacrals (Spencer 1951:102, fig. 10; Smith & Jell 1990:753, fig. 40). The madreporite is typically preserved, including portions of the stone canal (Spencer 1951:105, Smith & Jell 1990:762). Thus, a careful study of the arrangement of the ambulacral plates at the mouth frame (such as Smith & Jell 1990:fig. 47D) recorded with reference to the location of the madreporite would permit an analytical search for Lovén's law in the same manner as done in this paper (see Appendix).

The statement of Spencer & Wright (1966: U39) that in somasteroids the ambulacrals are "generally in opposite pairs but apparently alternating in some forms" conveys the wrong emphasis. In addition to *Archegonaster, Chinianaster* and *Villebrunaster* which have been mentioned above, alternating ambulacrals are described for *Ampullaster* (Fell 1963c:fig. 6A,D) and all of the Archophiactinidae (Spencer 1927:361). The recently described *Ophioxenikos langenheimi* has "proximal ambulacrals slightly offset, distal ambulacrals clearly offset across arm axis" (Blake & Guensburg 1993: 109). It is plausible that *Archegonaster* and other Paleozoic somasteroids with alternating ambulacral ossicles will eventually be shown to have the ambulacrals arranged in accordance with Lovén's law.

Asteroids.—Lovén's law has not yet been documented in asteroids. Although Spencer & Wright (1966:U13) stated "In this subclass the ambulacrals are invariably opposite one another, never alternating, as in somasteroids and early ophiuroids," this is not truly invariable. The situation in the Paleozoic Asteroidea echoes that of the somasteroids. The ambulacrals in some of the older species are not exactly opposite, but neither are they definitely alternating except perhaps near the tip of the arm. Spencer (1914:19) used the phrase "irregularly alternating" and expressed the view that this

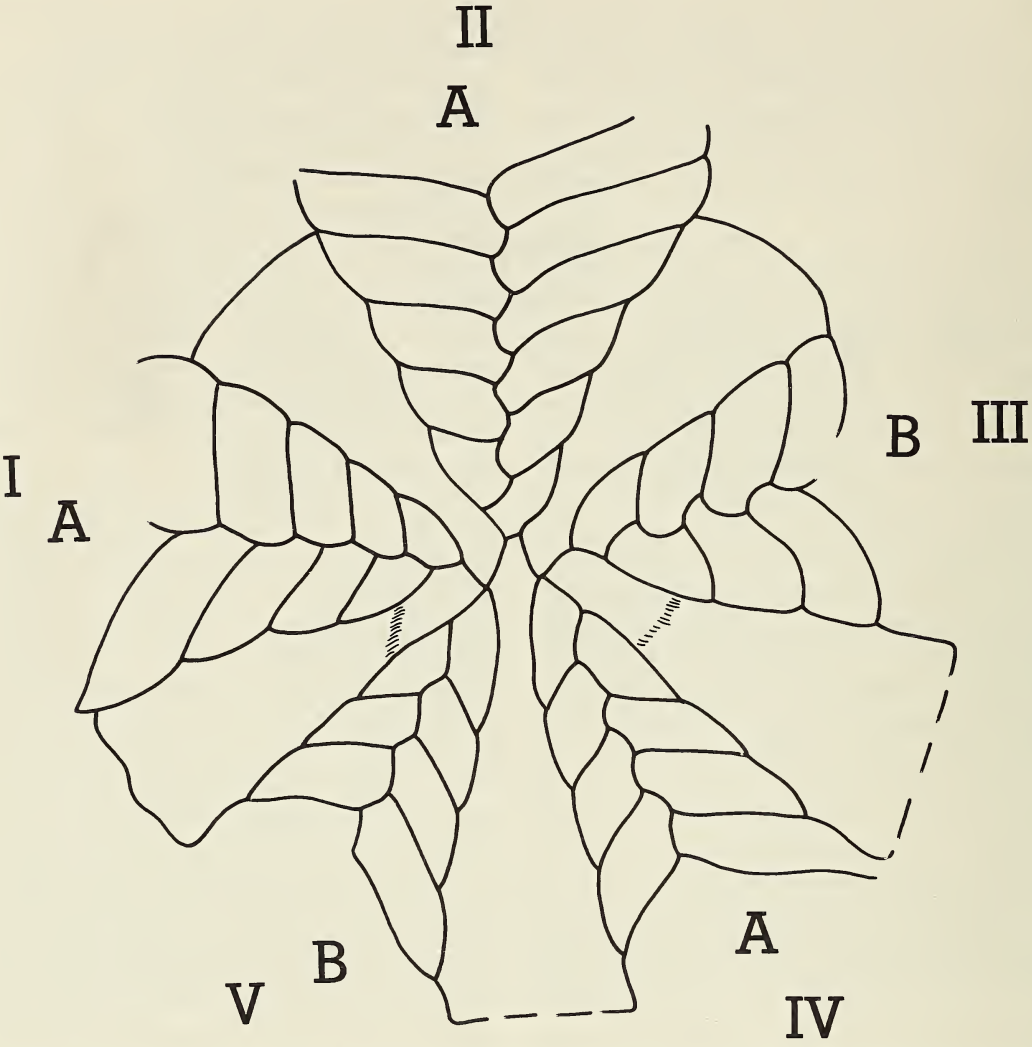

Fig. 3. Lovén's law in the Ordovician edrioasteroid *Astrocystites ottawaensis.* The cover plate half-series on the anticlockwise side of each ambulacrum is labeled as either in advance (A) or behind (B) the half-series on the clockwise side of the ambulacrum. The arrangement AABAB is Lovénian. Ray II is anterior; posterior interray IV/V contains the anus, hydropore and unpaired oro-tegminal plate. (Copied and annotated from Bather 1914b.)

was the primitive stock "from which two sets of forms arose, namely, those with opposite ambulacralia and those with definitely alternating ambulacralia."

Blake & Guensburg (1989:table 1, character no. 16) described the primitive character state of the "positions of ambulacral ossicles relative to one another across the furrow" as "weakly and locally alternate". They listed *Salteraster, Lacertasterias* and *Schondorfia* as having this primitive character state, and *Hudsonaster, Devonaster* and *Calliasterella* as having the derived character state of "opposite."

Other specific examples of early asteroids with "irregularly alternating" ambulacral plates are in the genera *Lanthanaster* and *Palasterina.* The holotype of *Lanthanaster cruciformis* [=*L. intermedius* (Schuchert, 1915); see Branstrator 1979] is very well preserved but has the region of the first few ambulacrals of each arm obscured from view by adambulacral spines. According to Branstrator (1972:68), "It is difficult to determine what the natural arrangement of ambulacral pairs across the ambulacral groove was when the animal was alive. The ambulacral ossicles of an arm appear (arm A, E) to have occurred in an alternate biseries, but the specimen is admittedly disturbed." Thus it is not possible to score the ambulacral plate arrangements of the arms as "A" or "B", but this will hopefully be possible in some future material. The madreporite is in an oral interradius. According to Spencer (1922:228) the holotype of *Palasterina bonneyi* Gregory [=*P. antiqua* (Hisinger); see Spencer 1922:228] has ambulacrals that "are opposite or slightly alternating in the proximal region, distinctly alternating distally"; a larger plate in one oral interradius "may represent the madreporite, but one cannot be certain of the madreporiform markings." It is plausible that *Lanthanaster, Palasterina* and other Paleozoic asteroids with "irregularly alternating" ambulacrals will eventually be shown to have the ambulacrals arranged in accordance with Lovén's law.

Edrioasteroids (Figs. 3, 4).—In Lower Cambrian *Camptostroma* and *Stromatocystites* the ambulacra are constructed of flooring plates arranged biserially and alternately (Paul & Smith 1984:470). This suggests searching for Lovén's law in edrioasteroids.

Order Edrioblastoida (see Smith & Jell 1990): Bather's illustration (1914b:201, fig. 6; Fay 1967:S289, fig. 172) of the exact sutures of the Middle Ordovician edrioblastoid *Astrocystites ottawaensis* Whiteaves, reproduced here as Fig. 3, shows that the arrangement of the cover plates conforms with Lovén's law (Hotchkiss 1978:543). It seems likely that the underlying ambulacrals are arranged in the same pattern as the cover plates. If the null hypothesis H0 is that the arrangement of ambulacrals in the different rays is a matter of chance and that the "A" arrangement is as probable as the "B" arrangement, then the probability of obtaining Lovén's law by chance alone in this specimen is $5/32 = 0.165$. Thus the one specimen does not allow us to reject the null hypothesis; however, the edrioasteroid that is next described turns out to provide the additional evidence that is needed to reject the null hypothesis and to draw a conclusion regarding Lovén's law in edrioasteroids.

Order Stromatocystitoida: Smith's (1985: 724, fig. 7) camera lucida drawing of specimen USNM 376690 of *Stromatocystites walcotti* Schuchert accurately presents the precise arrangement of the proximal ambulacral flooring plates including the oral area. [A portion of this drawing was published by Paul & Smith (1984:454, fig. 7).] Photographs of this specimen (Smith 1985: plate 88, figs. 3–5) corroborate the drawing. Essential to my interpretation is the information that Smith's drawing shows the interior of the oral surface. The plate arrangement is thus the mirror image of the plate arrangement that would be seen looking at the exterior oral surface. Using overhead transparency sheets and a photocopy machine, the image was reversed to simulate an exterior view of the oral surface (Fig. 4). Analysis of this external view shows that Lovén's law applies to this specimen.

The probability that Lovén's law will occur in this specimen by chance alone under the null hypothesis is $5/32 = 0.165$. Comparison shows that Lovén's law in this specimen of *Stromatocystites* has the same relation to the posterior interradius as in the specimen of *Astrocystites.* The probability that the same relation of Lovén's law to the posterior interradius will occur in this specimen of *Stromatocystites* as was observed in the specimen of *Astrocystites* by chance alone under the null hypothesis is $(5/32)$

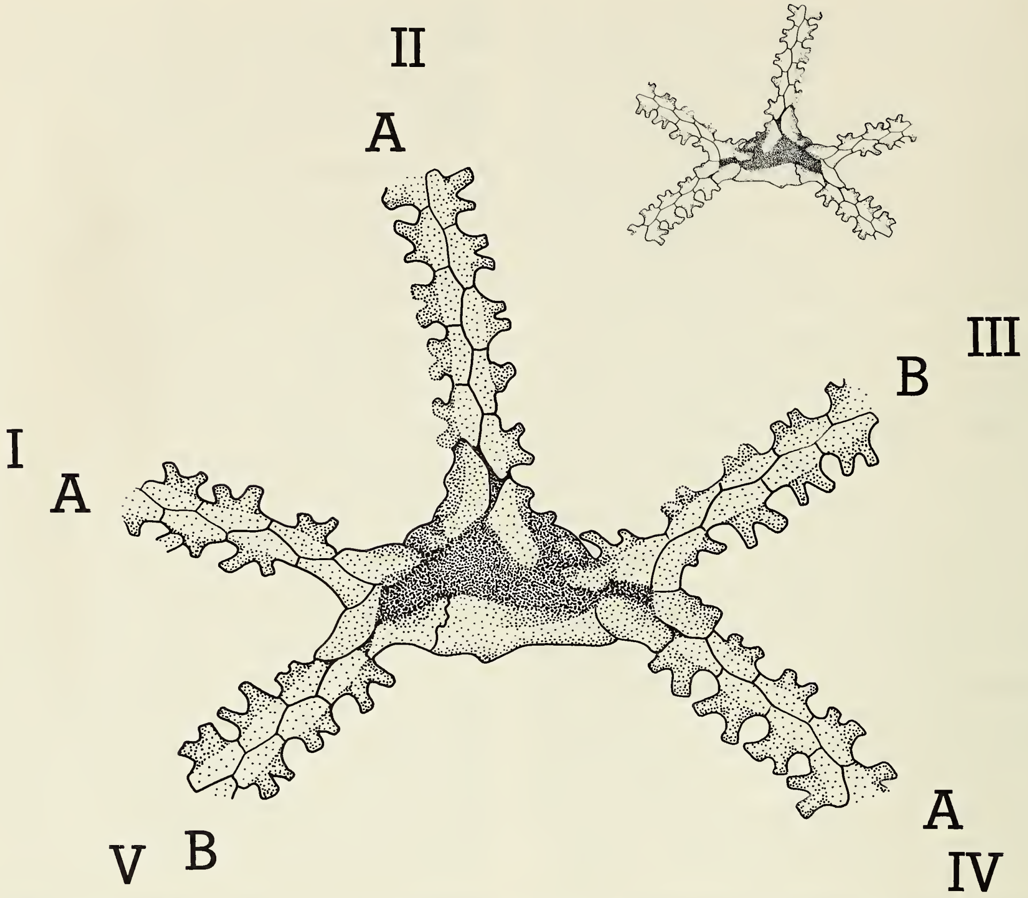

Fig. 4. Lovén's law in the Cambrian edrioasteroid *Stromatocystites walcotti.* Smith's drawing of the oral area and the proximal ambulacral flooring plates as seen from inside the test (small insert) has been reversed in the enlarged figure to simulate an external view. The flooring plate half-series on the anticlockwise side of each ambulacrum is labeled as either in advance (A) or behind (B) the half series on the clockwise side. The arrangement AABAB is Lovénian. Ray II is anterior; posterior interray IV/V contains the periproct and hydropore. The meaning of Lovén's law is interpreted from *Stromatocystites* to be a vestige of 2-1-2 pentaradiate organization, and to indicate a triradiate ancestry. (Copied and annotated from Paul & Smith 1984.)

(1/5) = 1/32 = 0.033. Thus, I reject the null hypothesis in favor of the belief that the observed arrangement of the ambulacrals is not due to chance alone. The new working hypothesis is that Lovén's law applies to *Stromatocystites walcotti* and to *Astrocystites ottawaensis* and that the posterior interradius is interradius IV/V in both species.

Ophiocistioids (Fig. 5).—Jell's (1983:230, fig. 14) camera lucida drawing of the oral surface of the well preserved holotype of the ophiocistioid *Gillocystis polypoda* shows the arrangement of the podial pores in the five ambulacral areas, together with the location of the madreporite and the periproct. Examination of Jell's drawing, reproduced here as Fig. 5, shows that Lovén's law applies to the arrangement of the podial pores, which alternate according to the AABAB pattern of Paleozoic ophiuroids. Based on Lovén's law, the madreporite of *Gillocystis* is in in-

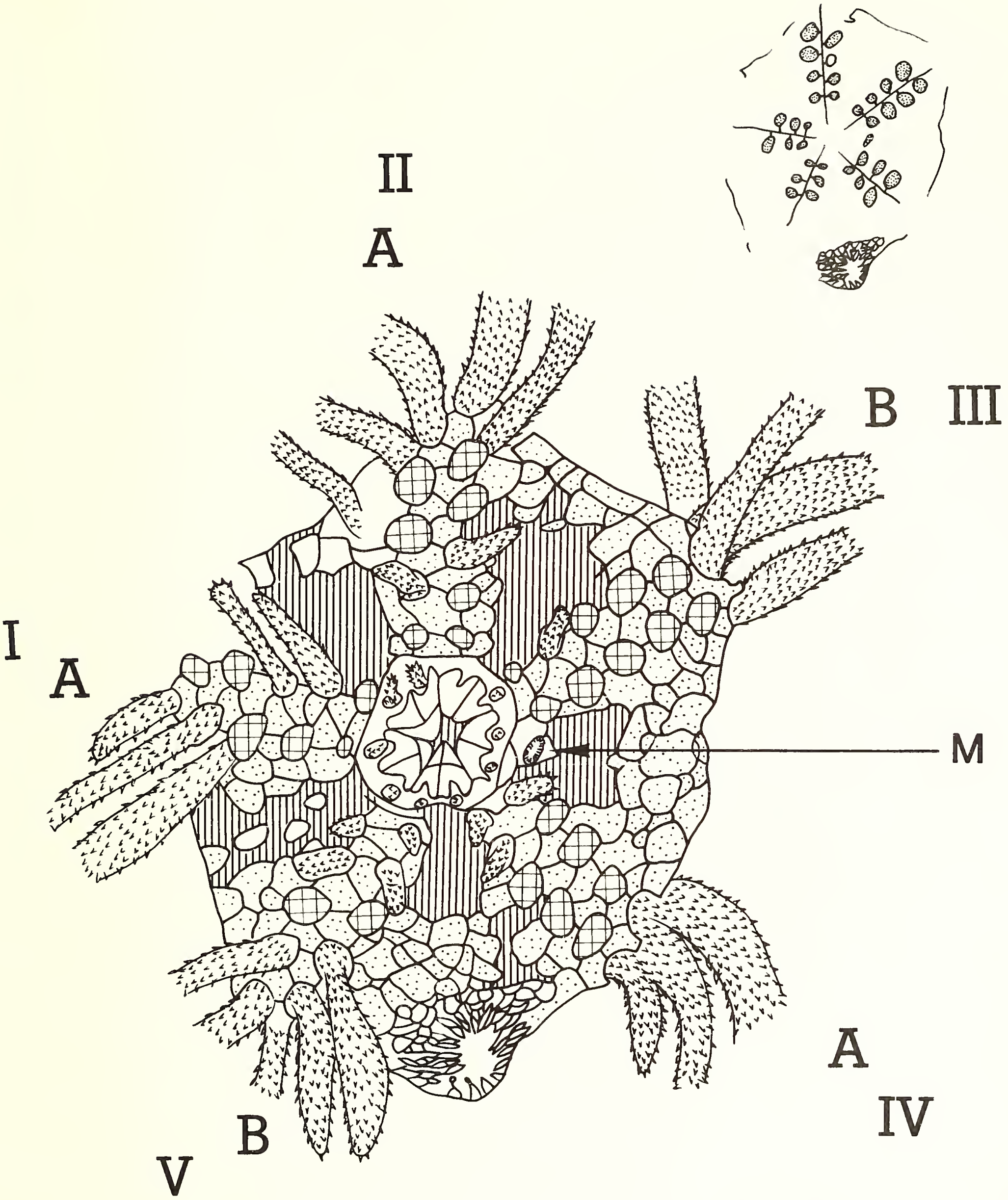

Fig. 5. Lovén's law in the Devonian ophiocistioid *Gillocystis polypoda* (oral side). Podial pores with no podia preserved are cross hatched. The small insert is a tracing of the podial pores and a reconstruction of the branches from the radial water vessel to the podia. The podial pores on the anticlockwise side of each ambulacrum are labeled as either in advance (A) or behind (B) the podial pores on the clockwise side. The arrangement AABAB is Lovénian. Ray II is anterior; posterior interray IV/V contains the periproct; right posterior interray III/IV contains the madreporite (M). (Copied and annotated from Jell 1983; areas where plates are not preserved are vertically lined or blank; positions of plates on the podia are stylized.)

terradius III/IV (as in ophiuroids), and the periproct is in the clockwise-adjacent interradius IV/V (as in edrioasteroids). The madreporite and periproct of *Sollasina woodwardi* also occupy clockwise-adjacent interradii (Haude & Langenstrassen 1976), but there are no observations concerning Lovén's law in this species.

In summary, Lovén's law is now known to apply to certain edrioasteroids, ophiuroids, echinoids, *Bothriocidaris* (considered a stem holothurian group by Smith 1984a) and an ophiocistioid. Thus, Lovén's law is not unique to ophiuroids and echinoids. As noted above, it is plausible that Lovén's law may eventually be found in the Asteroidea (such as *Lanthanaster*) and in the Somasteroidea (such as *Archegonaster*).

Symplesiomorphy of Lovén's Law

Is Lovén's law in ophiuroids, echinoids, edrioasteroids and ophiocistioids a similarity that is due to an ancestral character shared with a remote ancestor (symplesiomorphy)?

Because the relationships among echinoids, ophiuroids and edrioasteroids are distant, one must consider the likelihood (the probability under the null hypothesis H0) that these three lineages developed the same pattern of ambulacral plates merely by coincidence. [Ophiocistioids are not included because they cannot be treated as distantly related to echinoids: the jaw apparatus is so similar as to indicate that ophiocistioids were an offshoot from the echinoid lineage (Derstler 1985). Ophiocistioids may be grouped with echinoids or be substituted for echinoids, in this analysis.]

Of the 32 possible arrangements of alternating ambulacral plates around the peristome of a pentamerous animal, there are just 8 distinct patterns (Hotchkiss 1978): AAAAA, AAAAB, AAABB, AABAB, BBBBB, BBBBA, BBBAA, BBABA. Only the pattern AABAB conforms with Lovén's law. The patterns AAAAA and BBBBB can occur in an animal in only one arrangement, whereas five arrangements of each of the other six patterns can occur. Assuming that each of the arrangements confers equal fitness, the probability that three separate lineages of echinoderms would coincidentally develop the same pattern (not necessarily Lovén's law) of alternating ambulacral plates is given by $[2\times(1/32)(1/32)(1/32) + 6\times(5/32)(5/32)(5/32)] = 0.023$, which is an improbable coincidence. The probability that two lineages will coincidently develop Lovén's law given that the third lineage already conforms to Lovén's law is $(5/32)(5/32) = 0.024$, which again is an improbable coincidence. Therefore, I conclude that the presence of Lovén's law in echinoids, ophiuroids and edrioasteroids is not a chance coincidence. It is considered to be due either to a common inheritance (indicating ray homologies) or to convergent evolution (indicating a selective advantage to the pattern AABAB in each of its five arrangements but constituting a false guide to ray homologies because the five arrangements cannot be distinguished from one another). Lorenz (1974) has written a lucid account of how to distinguish convergent evolution (analogy) from common inheritance (false analogy), and here I follow the examples given in his paper very closely. In this method, if the improbable coincidental similarity has a very dissimilar function in the forms in which it occurs, then it is extremely improbable that the resemblance is due to parallel adaptation. The lifestyles of echinoids, ophiuroids and edrioasteroids are so obviously different that the functional morphology of their mouthframes and their proximal ambulacral plates must likewise be different. This makes the hypothesis H1 of a selective advantage that led to the convergent evolution of Lovén's law in these three classes very unlikely. On the other hand, the hypothesis H2 that in edrioasteroids Lovén's law is a manifestation of the 2-1-2 symmetry pattern and that in echinoids and in ophiuroids Lovén's law is a

Table 2.—Proposed ray homologies for echinoids, ophiuroids, ophiocistioids, edrioasteroids and asteroids. Roman numerals I, II, III, IV and V are used for homologous ray identifications based on recognizing Lovén's law. The numbering for edrioasteroids is different from that of previous authors (e.g., Bather 1914a, Regnéll 1966, Bell 1976a). The numbering for ophiocistioids is different from that of Jell (1983). Carpenter letters A, B, C, D and E for edrioasteroids are shown for reference (Moore & Fell 1966, Paul & Smith 1984). The ray homologies of asteroids are based on homologizing the location of closure of the ring canal in asteroids, ophiuroids and echinoids. Letters M, H, R and P mark the location of the madreporite (M) or hydropore (H), the location of closure of the hydrocoele crescent to form the ring canal (R), and the location of the anus/periproct (P).

Echinoids	II	M	III		IV	R	V	P	I
Ophiuroids	II		III	M	IV	R	V		I
Ophiocistioids	II		III	M	IV	R?/P	V		I
Edrioasteroids	II		III		IV	H/R/P	V		I
Edrioasteroids	A		B		C	H/R/P	D		E
Asteroids	A		B		C	R/P	D	M	E

vestige of this ancient symmetry, seems highly plausible. This result applies to the ophiocistioid as well. I exclude H1 and deduce from H2 that Lovén's law is a common inheritance that indicates ray homologies among ophiocistioids, echinoids, ophiuroids and edrioasteroids [see Note 2].

Ray Homologies Based on Lovén's Law

Ray homologies based on Lovén's law are proposed in Table 2. The location of the madreporite (M) or hydropore (H), the location of closure of the hydrocoele crescent to form the ring canal (R), and the location of the anus/periproct (P) are also shown in Table 2. Ray homologies for asteroids are included in Table 2 based on the proposal of homologizing the location of hydrocoele ring closure in asteroids with the IV/V interradius of ophiuroids and echinoids (Hotchkiss 1978). [The proposed ray homologies for asteroids are indicated by Carpenter letters in Table 2. Roman numerals are not used because asteroid ray identifications are not yet based on Lovén's law. Carpenter letters are assigned on the basis that the IV/V interradius of edrioasteroids is also the CD interradius.]

Location of hydrocoele ring closure.—With the ray homologies that are proposed in Table 2, the location of closure of the ring canal coincides in echinoids, ophiuroids and edrioasteroids and is postulated to coincide in asteroids. It is in interradius IV/V when the ray numbering is based on Lovén's law, and in the CD interradius of Carpenter's system. Data on the plane of hydrocoele closure for echinoids, asteroids and ophiuroids is taken from Bury (1889). Bather's opinion on the location of the plane of hydrocoele closure in edrioasteroids is accepted (1915:401): "in the primitive Pelmatozoön, so far as can be inferred from the embryology of *Antedon* and the anatomy of early forms, the closure of the hydrocoele was in what I [Bather] have termed the M plane [the plane containing the hydropore]." I have no data on the location of ring closure in ophiocistioids (but predict that it was in interradius IV/V).

Location of the madreporite.—With the ray homologies that are proposed in Table 2, the madreporite has a different location in four out of five groups. The one exception is that the madreporite is in interradius III/IV in both ophiuroids and ophiocistioids. Relocation of the hydropore/madreporite from interradius IV/V in edrioasteroids to interradius III/IV in ophiuroids and ophiocistioids may mean that the hydropore was duplicated on either side of ray IV in some ancestor. I accept the assumption of MacBride & Spencer (1938) that the madreporite in *Ectinechinus* and *Eothuria* (Upper Ordovician) lies in interradius II/III. Relocation of the madreporite in asteroids from its original position in edrioasteroids was already conceded by Bather (1915), with the explanation that the hydropore has only a secondary connection to the hydrocoele [see Note 3]. Evidence cited by Moore & Fell (1966) against the doctrine of a "firmly fixed location of the madreporite in all echinoderm groups" included a documented history of migrations of the madreporite to different portions of the echinoid apical system; the fact that some asteroids carry several madreporites scattered about the aboral side; and the fact that several euryalid ophiuroids have five madreporites, or else five hydropores, disposed one in each interradius.

Location of the periproct/anus.—With the ray homologies that are proposed in Table 2, the periproct/anus has the same location in edrioasteroids, asteroids and the ophiocistioid. It is in interradius IV/V when the ray numbering is based on Lovén's law, and in the CD interradius of Carpenter's system; this is the posterior interradius of edrioasteroids. Ophiuroids do not have an anus [see Note 4]. In echinoids the anus/periproct has migrated to a new location: in exocyclic echinoids it is in the posterior V/I interradius; in endocyclic Cidaroida and post-cidaroid groups the anus is incipiently displaced in the direction of the V/I interradius, as indicated by the tendency documented by Jackson (1912, 1927) for oculars V and I to be insert (Fell *in* Moore & Fell 1966). In the Saleniinae and some other Echinacea there has been a tertiary posterolateral movement of the anus within the apical system toward ocular I (Fell & Pawson 1966:U368); in *Temnopleurus reevesi* the anus is markedly excentric, midway between oculars I and II (Clark & Courtman-Stock 1976:fig. 251; Baranova 1982:115, fig. 1). I suspect that the position of the madreporite and the anus in the ophiocistioid *Gillocystis* represents the original condition for echinoids.

Bilateral symmetries.—When oriented according to Table 2, the 2-1-2 plane of bilateral symmetry of edrioasteroids and Lovén's plane of bilateral symmetry through the bivium and trivium of echinoids do not coincide. In exocyclic echinoids ray III is anterior, and in edrioasteroids ray II is anterior. It is clear that there have been multiple changes in symmetry during the evolution of echinoderms, such as from bilateral to radiate, and from radiate to bilateral (Bell 1976a:31, Caster 1967:S583, footnote) [see Note 5]. Vestiges of such changes may be retained in the morphology and ontogeny of the organism. The 2-1-2 plan developed from an original plan of triradiate symmetry (Bather 1900a, Fell 1966a, Sprinkle 1973). The hypothesis H2, established above, is that in edrioasteroids Lovén's law is a manifestation of the 2-1-2 symmetry pattern and that in ophiocistioids, echinoids and ophiuroids Lovén's law is a vestige of this ancient symmetry. In echinoids this result is particularly significant as it shows that Lovén's III-5 plane of bilateral symmetry, which Fell showed to be a fundamental feature of all orders of echinoids from the Cidaroida onward, is a new, secondary plane. The hypothesis H2 leads by deduction to the hypothesis H3 that ray II was the anterior ray in ancestral lines of the Echinoidea. The Ordovician *Ectinechinus* and *Eothuria* have elongated tests with anterior mouth and posterior anus; they are elongate not in Lovén's III-5 plane, but along von Übisch's II-4 axis of primordial symmetry, with ray II anterior (MacBride & Spencer 1938) [see Note 6]. These observations support the hypothesis H3 that ray II was the original anterior ray in both echinoids and edrioasteroids. Applied to the ophiocistioid *Gillocystis,* the hypothesis H3 that ray II was anterior leads to the deduction that the periproct was posterior.

Identification of the Axis of the Bilateral Larva in the Adult

Echinoderm larvae have a definite anterior-posterior axis and a marked bilateral symmetry. Proposals by von Übisch (1913, 1927), Lane & Webster (1967), Macurda (1980) and Smith & Arbizu (1987) as to which axis of an echinoderm postlarva corresponds with the axis of the bilateral larva are summarized in Table 3 [see Note 7].

As the working hypothesis H4 for the present study I assume that the relation of the axis of anterior-posterior organization of the larva to the axis of anterior-posterior organization of the imago has remained the same in echinoids, ophiuroids, edrioasteroids and ophiocistioids through inheritance from their common ancestor. Von Übisch (1913, 1927) showed that the anterior-posterior axis of the echinopluteus larva can be traced through metamorphosis by following the fate of the pieces of the larval skeleton. In this way he showed that the II-4 axis of the adult corresponds to the anterior-posterior axis of the bilateral larva, with ray II "anterior" in relation to the larva. His results were confirmed and expanded upon by Gordon (1929), Onoda (1931) and Emlet (1988, 1989) [see Note 8]. The ray homologies of Table 2 show that von Übisch's II-4 "axis of primordial symmetry" in echinoids coincides with the axis of the 2-1-2 pattern of bilateral symmetry of edrioasteroids. The 2-1-2 plan of symmetry in edrioasteroids expresses a left-right and an anterior-posterior symmetry, with ray II anterior and the anal interradius posterior. Using hypothesis H4 we therefore deduce that the anterior-posterior axis of the larva of edrioasteroids coincided with the anterior-posterior axis of the edrioasteroid, with ray II 'anterior' both in relation to the larva and in the imago. [Supporting indirect evidence is found in the many invertebrate groups that carry the anterior-posterior polarity of the larva through to the adult, including holothurians. Exceptions, when they occur, are probably due to secondary changes of symmetry, as shown here for postcidaroid exocyclic echinoids.]

Table 3.—Synopsis of some proposals concerning the identification of an axis in the adult that corresponds with the anterior-posterior axis of the bilateral larva [see Note 7].

Echinoids	II-4	(Übisch 1913, 1927)
Crinoids	E-BC	(Lane & Webster 1967)
Blastoids	D-AB	(Macurda 1980)
Edrioasteroids	A-CD	(Smith & Arbizu 1987)

Smith & Arbizu (1987) reported a situs inversus specimen of the edrioasteroid *Krama devonica* and proposed that the mirror plane for situs inversus in edrioasteroids coincides with the anterior/posterior plane of symmetry in the adult. Although their proposal may have seemed intuitively correct due to the 2-1-2 pattern of bilateral symmetry of edrioasteroids, it overlooked the fact stated by Swan (1966:414-416) that mirror images made using any axis across the animal will each produce identical situs inversus results. Thus, situs inversus by itself does not permit identification in the adult of the axis of symmetry of the larva. Nevertheless, it turns out that Smith's conjecture on the relation of the larval axis to the adult edrioasteriod is supported by the present study. [Conversely, the identifications of the larval axes proposed for crinoids by Lane & Webster (1967) and for blastoids by Macurda (1980) are not consistent with working hypothesis H4 and imply either an error in analysis, or a change in the axis relating the larva to the imago during the evolution of these groups.]

Larval Type of Ordovician Ophiuroids

It is interesting to see what can be inferred about the larvae of primitive Paleozoic ophiuroids. [Direct paleontological evidence on the larval forms of echinoderms is commented on in Note 9.] Smith (*in* Smith & Arbizu, 1987) inferred a bilateral larva for edrioasteroids based on a situs inversus specimen of *Krama devonica.* In the same paper Smith referred to mirror image forms of the carpoid *Peltocystis cornuta.* The occurrence of mirror image forms is clear evidence of the 'handedness' that comes from deriving the water vascular system from the left hydrocoele of a bilateral larva in normal larvae and from the right hydrocoele in cases of situs inversus. It seems highly likely that not only edrioasteroids but also the derived asterozoans had a bilateral larva.

The extended arms of the ophiopluteus depend on the skeletal rods for their support (Strathmann 1988:60). The acquisition of skeletal rods by echinoderm larvae was explained by Strathmann (1993:91) as an example of heterochrony (or adultation) as follows: "Echinoderms have a type of calcite skeleton unique to the phylum. Within the echinoderms, the calcite skeleton does not develop until metamorphosis in the asteroids, but in the echinoids and ophiuroids, deposition of calcite begins in the embryo and produces supporting skeletal rods in the larva. This distribution of traits suggests that the skeleton originated in postlarval stages and that the pluteus originated by accelerated skeletal development." In comparing the pluteus skeleton of echinoplutei and ophioplutei, Strathmann (1988:62) commented that "the formation and branching of the skeleton is so different between classes that homology can be questioned." He suggested (in litt.) that independent evolution of arm rods in ophioplutei and echinoplutei is the simplest and most plausible hypothesis at this time.

Smith (1984a:figure 9.4) listed the development of the pluteus type of larva and also Lovén's law of heterotropy as two of the synapomorphies [shared derived character states] between echinoids and ophiuroids [see Note 10]. This was reiterated by Paul & Smith (1984:469): "Echinoids share a number of advanced morphological innovations with Ordovician ophiuroids. These include . . . oral plating in obedience to Lovén's law and (judging from living animals) . . . the development of a pluteus larva with a skeletal framework." Ordovician ophiuroids belong to the prephrynophiurid orders Oegophiurida and Stenurida. I favor a different hypothesis based on the proposal by Fell (1966b:131) that the ophiopluteus is a postphrynophiurid development.

In a series of papers, Fell (1948, 1963b, 1963c, 1966a, 1967) expressed his view that the pluteus arose independently in ophiuroids and echinoids and that possession of the pluteus larval form is not evidence of a close phylogenetic relation between ophiuroids and echinoids. He supported his views with data from embryology and larval forms and from the fossil record and adult anatomy. Differences between the ophiopluteus and the echinopluteus were summarized by Smith (1984b:452–453) as follows: "Neither the processes nor the skeleton are identical in echinoids and ophiuroids. The ophiopluteus has no pre-oral processes and the main locomotory processes that develop early on are the posterolateral ones, whereas in the echinopluteus, elongate pre-oral processes are present, and the main locomotory processes are the post-oral ones. The posterolateral processes either appear much later in development and remain small or are absent altogether. The ophiopluteus has just two centers of calcification from which calcite rods grow, one on either side, whereas the echinopluteus has five, two on the left, two on the right, and an anterior V-shaped rod for the pre-oral processes." Fell (1948:83) described the same principal differences in the ophiopluteus: "the preoral arms of the echinopluteus are not represented; the internal skeleton takes the form of a pair of calcareous rods in the body, each sending branches into the four arms on its corresponding side; the posterior transverse rod is not represented." These differences support the opinion already accepted by de Beer (1940:373) that this is a case of similarity through convergence (see also Mortensen 1921:227).

Fell described the development of "Kirk's ophiuroid" (Fell 1941a), made observations on development in *Ophiomyxa* (Fell 1941b), and described the development of *Amphi-*

pholis squamata (Fell 1946). Fell (1941a: 416, 1948:fig. 4) observed that there was no trace of larva in the development of Kirk's ophiuroid and initially placed this form of development as the end member of his series of the regression of metamorphosis (Fell 1945:90, fig. 20, 1948:98, fig. 6). Subsequently, he identified Kirk's ophiuroid as *Ophiomyxa* sp. (Fell 1963b:fig. 15 caption, 1966b:139, 1967:fig. 25 caption), and he identified *Ophiocanops fugiens* as a surviving oegophiurid (Fell 1962). Fell then reexamined the development of the primitive Phrynophiurida and wrote (Fell 1963c:481): "Although we still know nothing of the embryology of *Ophiocanops,* many features of its anatomy declare its affinity to the Ophiomyxidae, a group of ophiuroids in which absolutely direct development occurs, without any trace of a larva at all. On the other hand, those genera of Ophiuroidea which have vestigial larvae have now been shown to fall in families of relatively late derivation, from groups which have pelagic larvae. They are groups with numerous secondary features in the skeleton, far removed from the archaic forms with somasteroid-like features. Thus it is now extremely probable that there are two quite distinct types of direct development in ophiuroids, one ancient, with no vestige of larva, the other secondary and showing both by the vestigial larva and by the characters of the skeleton that it is of late origin. I now suspect that the pluteus larva will eventually be proved to be a feature evolved by ophiuroids after the separation of ophiuroids from the somasteroid line, and that the pluteus of echinoids is an entirely independent development of that group." Fell (1966a:237, 1966b: 131) proposed that the ophiopluteus evolved in the order Ophiurida and was not the original larval form of ophiuroids. The Ophiurida are shown on paleontological and morphological evidence to be a late grade of evolution (Fell 1963b:410, Table 2).

Fell's work was reviewed and extended by Dorothy Patent (1970) who described the early embryology of the basket star *Gorgonocephalus caryi.* The embryos reached a pentagon stage, without podia, before dying. Further development may occur in nature inside polyps of the alcyonarian *Gersemia.* She reported (1970:262): "At no time did cilia or other locomotory structures develop. The development of *G. caryi* does not resemble that of any other ophiuroid studied. There is no trace of a pluteus, and it is postulated that the pluteus evolved after the Phrynophiurida and the Ophiurida were differentiated."

Strathmann (1974:334-336, 1975, 1978) has persuasively argued that non-feeding larvae appear to be derived from feeding larvae, rather than the reverse. He noted that planktotrophic development appears to have been lost entirely from all lines of descent in the order Phrynophiurida [see Note 11]. He reasoned that because "members of the order Ophiurida with lecithotrophy probably do not include the ancestors of the Phrynophiurida," lecithotrophic development must have evolved independently in the Phrynophiurida or their ancestors. In other words, the Phrynophiurida must have had a planktotrophic ancestor.

Combining the proposals of Fell, Patent, Strathmann, and Smith, I speculate that the larval type of the stem phrynophiurid was a bilateral planktotroph, but not yet an ophiopluteus. This hypothetical sequence is illustrated in Fig. 6, which includes the notion (following Fell 1962) that *Ophiocanops* may be a surviving representative of the stem group of the Order Phrynophiurida.

Ray Homologies and 2-1-2 Symmetry

Concerning the 2-1-2 pattern of ambulacra in Cambrian echinoderms, Paul & Smith (1984:470) stated that "in all of these early pentaradiate echinoderms, the single unbranched ambulacrum lies opposite the interambulacrum that contains the periproct, hydropore and gonopore (when they can be recognized)." They make it obvious

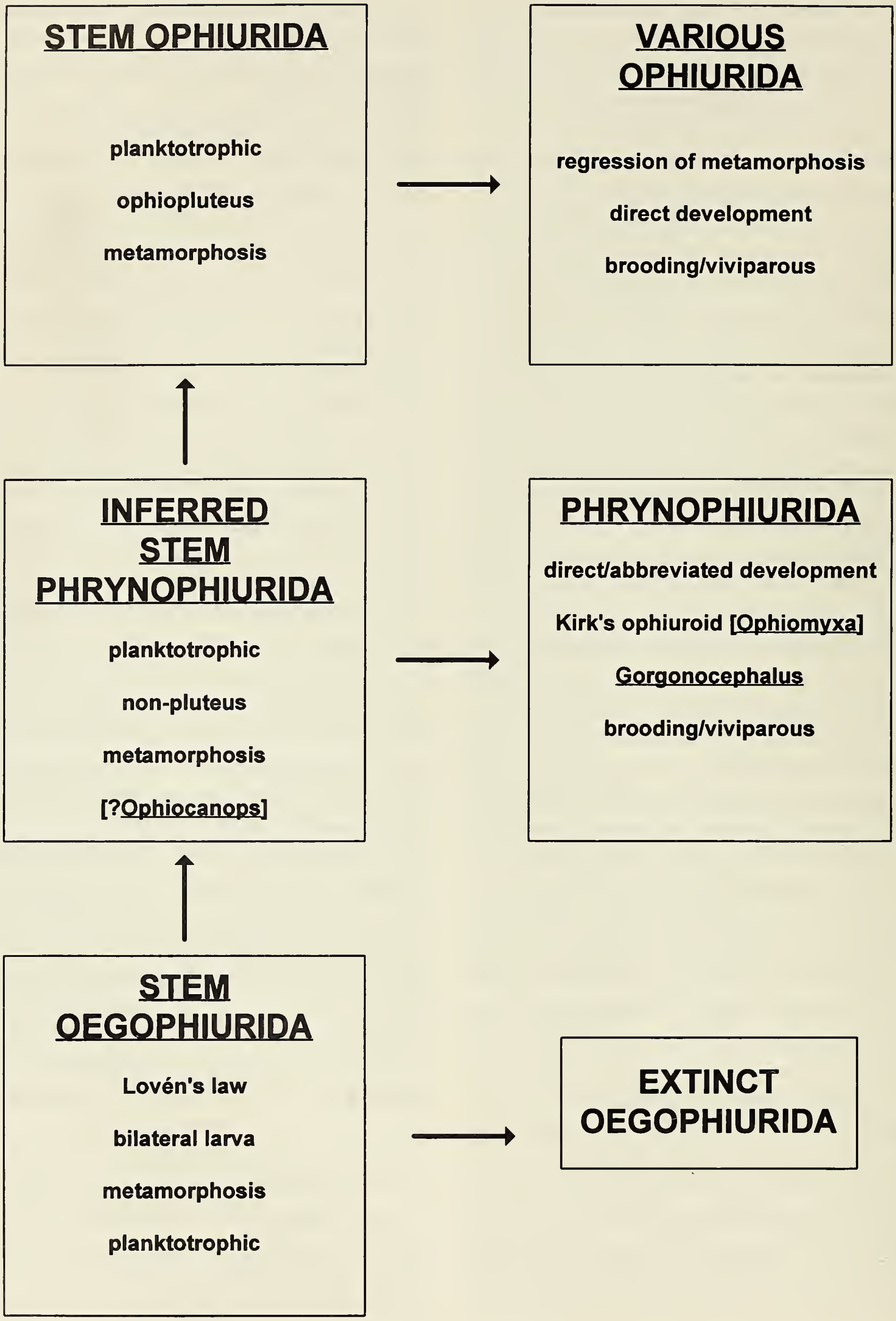

Fig. 6. Inferred evolution of ophiuroid larvae and ophiuroid development. The larval type of the stem phrynophiurid is inferred to have been a bilateral planktotroph, but not yet an ophiopluteus. The ophiopluteus is a postphrynophiurid development. Hence the similarity of the pluteus larvae of ophiuroids and echinoids is judged a homeomorphism.

that the solution to ray homologies is to identify the 2-1-2 pattern in the descendent groups. The present study shows that echinoids, ophiuroids, edrioasteroids and an ophiocistioid have retained the imprint of the 2-1-2 pattern of bilateral symmetry in the form of Lovén's law. Accordingly, ray homologies based on the 2-1-2 pattern of Lovén's law, as presented in Table 2, satisfy the requirements established by Paul & Smith.

Citing Lovén (1874), Fell (*in* Moore & Fell 1966) interpreted Lovén's law of heterotropy as a correlate of Lovén's plane of bilateral symmetry. Because the basicoronal plates of *Bothriocidaris* conform with Lovén's law of heterotropy, this (supposed) correlation enabled Fell to write (p. U124): "The archaic *Bothriocidaris* (Ord.) at least already exhibited the same anteroposterior plane of symmetry that is manifested in the Cidaroida and in post-cidaroid groups, as indicated by the potential, incipient, or consummated migration of the anus into interamb 5" [see Note 12]. It now turns out from the discovery of Lovén's law in the Cambrian edrioasteroid *Stromatocystites* that Lovén's law is more ancient than Lovén's plane of bilateral symmetry. Lovén's law appears to be a manifestation of the plane of symmetry of 2-1-2 pentaradiate echinoderms, and Lovén's plane is a superimposed secondary development in echinoids. In Lovénian symmetry, ray III is anterior; in 2-1-2 symmetry it is ray II that is anterior.

Adult Symmetry and Phylogeny

Bell (1976b:1017) studied the early growth stages of edrioasteroids and showed that "edrioasteroid ontogeny bespeaks a primitive triradiate symmetry that was later modified to a pentaradiate plan." He remarked that echinoids and Asterozoa, among others, show no apparent signs of triradial symmetry. He concluded (p. 1018) that "If some classes of echinoderms are primitively triradiates . . . and if, in contrast, others are indeed primitively pentaradiates, then a major phylogenetic dichotomy occurred early in the history of this phylum." The current research helps to remove this dichotomy and to unify the evolutionary history by showing that Lovén's law in echinoids, ophiuroids and ophiocistioids is a manifestation of the triradiate symmetry (2-1-2 pattern) of edrioasteroids.

The current research helps to answer questions posed in my first study: whether Lovén's law independently evolved in echinoids and ophiuroids, or whether it is indicative of a recent common ancestry between echinoids and ophiuroids, or whether Lovén's law is fundamental to the ground plan of the phylum (see Hotchkiss 1978). The probabilities calculated above show that the presence of Lovén's law in echinoids, ophiuroids, edrioasteroids and ophiocistioids is not a chance coincidence. Because edrioasteroids and ophiocistioids also obey Lovén's law, it is clear that Lovén's law is not evidence of a recent common ancestry between echinoids and ophiuroids [see Note 13]. My suggestion that Lovén's law might be fundamental to the ground plan of the phylum was based on the 'Treatise' classification (Fay 1967) of *Astrocystites* in the Class Edrioblastoidea, within the Subphylum Crinozoa, making it seem totally unrelated to either echinoids or ophiuroids. The situation is different now that Smith & Jell (1990) have shown that *Astrocystites* is an edrioasteroid. The result of this change is that all of the echinoderms in which Lovén's law is now known belong to classes that are placed by Smith (1984b) in the Subphylum Eleutherozoa. Therefore, I abandon my earlier suggestion and offer the more restricted hypothesis H5 that Lovén's law is fundamental to the ground plan of the clade Eleutherozoa (sensu Smith 1984b).

Mortensen's studies led him to regard *Bothriocidaris* "as a specialized offshoot from the Diploporite Cystids" (Mortensen 1928:93, 1930), and this caused him to search for Lovén's law in diploporite cystoids. He regretted that he did not have any definite proof of Lovén's law in diploporite cystoids, but he argued that "it is not so very wild a suggestion"; he also reasoned that if Lovén's law is due to mechanical reasons, then it might have arisen independently in *Bothriocidaris* (Mortensen 1928: 107, 1930:343). I have examined the illustrations in the 'Treatise' and other sources, hoping to detect Lovén's law in cystoids. I did not find Lovén's law but found an altogether different pattern. The 2-1-2 ambulacral areas of Blastozoa such as the cystoids *Cystoblastus, Bulbocystis, Protocrinites* and *Glyptosphaerites,* and the eocrinoids *Rhopalocystis, Mimocystites* and *Ascocystites* are all of the same "handedness", so that if one gives off a brachiole on the left side before any arise on the right, then it is that way in each of the ambulacral areas. This blastozoan pattern is so regular in its own way that it leads to the hypothesis H6 that there are at least two distinct constructions of 2-1-2 symmetry: that seen in the Blastozoa, and that seen in the Eleutherozoa. [Derstler (1985) maintained the crinoids as a 2-1-2 clade distinct from blastozoans and edrioasteroids, and so possibly there is a third construction of 2-1-2 symmetry (not studied here).] These observations support Derstler's working hypothesis that the transition from triradiate to 2-1-2 symmetry may have occurred independently in these groups.

[Epilogue: Thanks to Dr. David L. Pawson I received a copy of a new paper by Dr. Reimund Haude (1994) on fossil Holothuroidea (Eleutherozoa) just before returning this manuscript to the editor (February 1995). I wish to bring this paper to the attention of readers and to comment on its significance to the present results. Dr. Haude has observed in the pharyngial ring of a Devonian holothurian that the radial pieces have a left and a right anterior process, and that in each radial element one or the other of these processes is pierced by a pore. The pattern of these piercings is summarized by a RRLRL rule, where R stands for the right anterior process being pierced, and L for the left anterior process. Dr. Haude noted that this pattern might very well reflect Lovén's law in the ambulacral plates of the ancestor to the holothurians. Thus his observations support the hypothesis H5 that Lovén's law is fundamental to the clade Eleutherozoa. The relation of the RRLRL rule to the madreporite or to the bivium and trivium of holothurians is not yet known, but it seems likely that this information will be determined in the near future. At that time it will become possible to add holothurians to the table of ray homologies.]

Notes and Acknowledgements

Note 1.—When the solution to the question of ray homologies among the classes of echinoderms has been worked out, it will suffice to have a single system of ray identifications. At the present time there are several conflicting suggestions that purport to answer the question of the true ray homologies, including the one presented in this paper. In this circumstance it may be advantageous to have both Carpenter letters and Roman numerals available for the labeling of the rays. I recommend use of Roman numerals for ray identifications that are based on Lovén's law. Roman numerals were established for echinoids by Lovén (1874). Lovén (1874: pl. 53) numbered the rays of asteroids based on identifying the location of the madreporite with the II/III interradius of echinoids; Lovén (1874:88, figure) correctly observed the location of the asteroid anus, drawing it in interradius I/II adjacent to the madreporic interradius II/III. Gemmill (1914:276; see also Chadwick 1923:9) numbered the rays of asteroids based upon the location of the closure of the hydrocoele ring, beginning with I at the anterior (or dorsal) horn of the hydrocoele crescent, and proceeding clockwise in oral view. This placed the madreporite of asteroids in interradius I/II and the anus in V/I. Bather (1914a; see also Regnéll 1966, Bell 1976a:9) identified the ambulacra of edrioasteroids with Roman numerals: I is left posterior, II is left anterior, III is anterior, IV is right anterior, and V is right posterior; the anus and hydropore are in interradius V/I. Spencer used Roman numerals in his monograph of the Paleozoic Asterozoa. His text-figure 1 (Spencer 1914:5) of the "Pelmatozoan ancestor of the Asterozoa" shows the water pore in interradius IV/V and the numerals I through V in clockwise manner when looked at from the oral surface. His text-figure 59 (Spencer 1916:103) of *Mesopalaeaster*(?) *ketley* has the madreporite in interradius I/II and numerals I through V applied in clockwise manner when looked at from the aboral (apical) surface. I believe that he used the latter method to number the rays of *Protaster sedgwicki* (Spencer 1934:459–460). Hahn & Brauckmann (1981: 9) used the madreporite of the ophiuroid *Chattaster hueffneri* [as *C. dillensis*] to identify the right anterior interradius (by analogy with echinoids; see Haude 1982:25). Jell (1983) numbered the rays of the ophiocistioid *Gillocystis* with the periproct in interradius V/I (by analogy with echinoids).

Note 2.—A consequence of this finding is that Asterozoa with alternating ambulacrals must have been ancestral to those with opposite ambulacrals. In fact, this is exactly what Fell (1963c:476) had concluded from the arrangement of the ambulacrals in *Chinianaster* and *Villebrunaster:* "Since we have ascertained that the ambulacral ossicles alternate near the tip of the arm, and in the young stages of *Chinianaster,* it follows from Jackson's (1899, 1903) so-called "law of localized stages" that the opposite condition of ambulacral ossicles must have been derived from an original alternating condition. This alternating condition was retained in *Archegonaster,* in some Paleozoic asteroids, and in some of the Paleozoic ophiuroids."

Sollas & Sollas (1912:223) reported difficulty in deciding whether the free, partly alternating ambulacral ossicles of primitive Paleozoic ophiuroids represented alternation that was natural or that was due to displacement of free opposite ambulacral ossicles either during life or after death. The current research helps to resolve this difficulty by determining that the progression of evolution of the ambulacral ossicles in ophiuroids must have been from an alternating arrangement that obeyed Lovén's law, to a partly alternating condition, ultimately leading to ossicles that are paired. As noted by Sollas & Sollas, the paired ossicles were at first free, and later they connected and fused to form vertebrae.

Fell (1963b,c) removed the asterozoans from the Eleutherozoa when he proposed that somasteroids with metapinnular structure evolved from crinoids. The evidence presented here places the constraint of improbable chance coincidence or parallel evolution of Lovén's law onto that proposal. The cumulative evidence from the present study, from reanalysis of plate homologies (Hotchkiss 1993), and from the Middle Cambrian Burgess Shale crinoid *Echmatocrinus* (Sprinkle 1973) is that the crinoid arm and the somasteroid ray do not appear to be comparable structures. The conclusion that Lovén's law is a plesiomorphic character supports the working hypothesis of Bather (1900b) and Smith & Jell (1990) that the ancestry of sea stars is among edrioasteroids.

Note 3.—It seems that in asteroids the madreporite does not develop in the same position that it does in ophiuroids, because assigning the location of the closure of the ring canal to interradius IV/V places the asteroid madreporite in V/I. This puts an unexpected gulf between the ophiuroids and the asteroids. Bather (1915) tried to solve the problem of deriving the asteroids from edrioasteroids by invoking "a shifting of the whole hydrocoele [such] that each lobe of it becomes applied, not to the ray to which it would (especially on any homology with

Pelmatozoa) naturally belong, but to the neighboring ray." Bather also had to propose (p. 401) that "Such shifting need not involve the hydropore, with which the hydrocoele has only a secondary connection." Embryology is beyond the scope of this paper and beyond my own expertise. However, it seems to me that the best explanations concerning the relocating of the madreporite during the evolution of the echinoderm classes will most likely be associated with evolutionary changes that occurred in the larvae and in the process of metamorphosis. Perhaps the data are already available. [One of my own unsuccessful attempts at a solution may be worth noting. We know that loss or gain of rays can occur at the ends of the hydrocoele crescent during metamorphosis (Hotchkiss & Seegers 1976). It seemed to me that this offers the possibility of losing and gaining rays such that the ray count remains at five. This could change the relative positions of the madreporite and the anus in edrioasteroids, asteroids, echinoids and ophiocistioids. However, no reasonable solution came from my attempts and I am now convinced that this has not happened. Such an event is not consistent with retaining the imprint of 2-1-2 symmetry represented by Lovén's law in ophiuroids, echinoids and ophiocistioids.]

Note 4.—In discussing the Echinozoa and the Asterozoa, Fell wrote (1963b:426): "There is no anus in archaic asteroids, nor in any ophiuroid, nor is it known in any somasteroid. An aboral anus occurs as a late acquisition in post-luidiid asteroids. On the other hand, fossils show that an aboral anus is a fundamental character of echinoids, present in the earliest forms. All holothurians have an aboral anus." In the asteroid lineage the anus arose "after the initial differentiation of the Astropectinidae, so it is not an original feature of the family, and is lacking in some members" (Fell 1963b: Table 1). In Smith's (1988a:fig. 7.2, 7.3) cladograms, the anus was present in the edrioasteroids, became missing in the stem somasteroids, reappeared later in the asteroid line, did not reappear at all in the ophiuroid line, but reappeared in the echinoids, ophiocistioids and holothuroids as a post-stem ophiuroid development. In the experience of Smith (1988b:819): "The presence of an anus is difficult to detect in some fossils, but does genuinely appear to be absent in primitive asteroids and ophiuroids". Blake (1987: 499, 506–507, 522; 1988) suggested that loss of the anus occurs rather readily and that the absence of rectal caeca and of an anus in the Paxillosida is a derived character state. Kesling (1962) reported a probable anal pyramid in *Protopalaeaster narrawayi* [Middle Ordovician]; Kesling & Strimple (1966) observed in the central plate of *Calliasterella americana* [Missisippian, transferred to *Calyptactis* by Chesnut & Ettensohn 1988] a notch that may have bordered the anus; both reports locate the anus and the madreporite consistent with Table 2. An ophiuroid from the Silurian of Gotland that is reported to have an anal cone is under study by Regnéll (1973:fig. 4, cited by Franzén 1979:220). Accepting this report means that the anus was reacquired by a Silurian ophiuroid which appears not to have left any descendants (at least none with an anus). From examination of Ruedemann's specimen of *Stenaster salteri* (= *S. obtusus*) with a supposed anal pore (Ruedemann 1916:54, plate 11, fig. 1) (Kilfoyle 1954:199, specimen NYSM 7744), I think it probable that the pore is an artifact from weathering. A careful search for an anus in fossils of Paleozoic asteroids and ophiuroids should continue to be made. It should be looked for not only on the aboral surface, but also on the oral surface (as in edrioasteroids) and on the interradial margins of the disc, as found in the ophiocistioid *Gillocystis* (Jell 1983).

Note 5.—Evidence of multiple changes in symmetry in echinoids includes the markedly oval tests of the Echinometridae (Grabowsky 1994). The axis of elongation plainly differs from that of spatangoids and other exocyclic echinoids, yet does not alter the tendency for oculars I and V to become insert (Fell *in* Moore & Fell 1966:U124). Also in echinoids, the markedly oblique peristome in certain cassiduloids and holectypoids may be mentioned (Rose 1976:303). The oral side of *Amblypygus merrilli* figured by Clark & Twitchel (1915:plate 76) displays a very evident bilateral symmetry of the peristome and the ambulacra about the II-4 plane, whereas the periproct is elongate and symmetrical in the III-5 plane. [Roman (1957) pointed out that the bilateral symmetry of *Echinolampas* is just external: the internal organs are not bilaterally arranged, and upon taking measurements the test itself is found to be not perfectly symmetrical.]

In crinoids may be mentioned *Comatula pectinata* showing a relative elongation of most of the 'anterior' arms (i.e., those corresponding to the side of the disc opposite the anus) (Clark 1977:Fig. 6b). Also, the recumbent bent-crown Calceocrinidae are bilateral in the E-BC homocrinid plane (Lane & Webster 1967, Brower 1985). [In *Holopus rangii* the position of the bivium and trivium of shorter and longer rays differs among specimens (Donovan 1992:668).]

In holothurians may be mentioned the Antarctic psolid *Ekkentropelma brychia* which has the mouth and anus of the U-shaped body displaced at 90 degrees to the usual holothurian plane of bilateral symmetry, while the sole is morphologically ventral, as usual. "Thus, the sole is functionally lateral in position, and apparently the animal is well adapted to attaching itself to vertical surfaces" (Pawson 1971:113).

In asteroids may be mentioned reports of leading arms in locomotion, of arm preferences in righting behavior, and also bilateral patterns of ray addition in some multiradiate starfish (see review in Hotchkiss & Seegers 1976). Also, on the aboral surface of *Luidia clathrata* there is a conspicuous line of dark coloration on the midline of each arm and in just one interradius (the madreporic interradius); these dark lines connect not to a central point but in a bilaterally symmetrical pattern that suggests a trivium and a bivium of rays (Gray et al. 1968: 139, figure 8A).

In ophiuroids may be mentioned *Asteronyx loveni* with two nonadjacent thick and long arms and three intervening thinner and shorter arms, although their orientation relative to the madreporite has not been described (Fujita & Ohta 1988, Irimura 1991). [The orientation relative to the madreporite of a similar pattern found in early growth stages of *Ophiophragmus filograneus* and *Amphiura filiformis* differs among specimens (Turner 1974, Muus 1981).] As another example, the juvenile *Ophiomastix flaccida* illustrated by Clark (1921:138, plate 13, figure 2) shows a color pattern with unmistakable bilateral symmetry. The color pattern of *Sigsbeia lineata* suggests imperfect bilateral symmetry (Lütken & Mortensen 1899:plate 20, figure 8).

Note 6.—Concerning Paleozoic echinoids with 'irregular' tendencies, the orientation of the oblong test of *Hyattechinus beecheri* has not yet been determined (Jackson 1912). The supposedly posterior anus in the Silurian *Palaeodiscus* and *Echinocystites* was shown by Hawkins & Hampton (1927) to be in the usual aboral, endocylic position of the Regularia. The elongate shape of *Ectinechinus* and *Eothuria,* although questioned as possibly due to post-mortem distortion by Kier (1965:442), is provisionally accepted herein because of the exceptional interest that attaches to the observation of MacBride & Spencer (1938) that the plane of elongation follows von Übisch's primordial plane of symmetry. Also of interest is the observation by Fell (1965:6) that "The earliest Echinoidea, such as *Eothuria,* possessed a multiplated, flexible spirally twisted body wall, similar to that of the Helicoplacoidea, and perhaps inherited from a helicoplacoid ancestry."

Note 7.—Evidence of the axis of the bilateral larva in the adults of *Asterias rubens* has been adduced from behavioral studies

(Smith 1950:216): "The tendency for arm II to dominate the locomotory pattern is not to be ascribed to any obvious organizational feature such as greater arm length or a greater number of podia. It appears rather to reflect some intrinsic feature of nervous organization such as, perhaps, the retention of traces of the bilateral symmetry of larva." [I regret that I do not know how Smith assigned Roman numerals to the rays.]

From anatomy and embryology (Lane & Webster 1967): "The homocrinid (E-BC) plane of bilateral symmetry in the crown of some monocyclic inadunate and flexible crinoids is postulated to be a relict expression in adults of the dorso-ventral symmetry plane of the doliolarian, free-swimming, larval stage."

From embryology (Grave *in* Brooks & Grave 1899:89, pl. I, fig. 6): In *Ophioderma brevispina* stage "C" larvae the hydrocoele is "a horseshoe-shaped structure astride the oesophagus," and "half of it lies to the right of the median sagittal plane of the larva and half to the left. Radial canal 3 lies in this plane and points directly toward the anterior of the larva." [The relation of the lobes of the hydrocoele crescent and of the plane of hydrocoele closure to the axis of the larva may provide a means of tracing the larval axis through to the adult, and should be documented wherever possible; perhaps more of such data already exist.]

From teratology (Macurda 1980:1161): "Abnormalities which were present in the bilaterally symmetrical larvae would be carried forward during metamorphosis to the pentameral adult and should have a bilateral distribution. . . . The data from this study appear to be supportive of the AB-D plane as being the larval symmetry plane in blastoids." [See also Macurda 1964, 1978]

Note 8.—The left side of the larva becomes the oral surface, and the right side becomes the aboral surface. Hence the plane of symmetry of the echinopluteus is at right angles to von Übisch's plane of primordial symmetry in the adult. The axes of symmetry are coincident even though the planes are at right angles (Onoda 1931:126). Crystallographic studies of echinoid ocular and genital plates, summarized and extended by Emlet (1988, 1989), confirm von Übisch's plane of primordial symmetry in many genera for which the development has not yet been directly observed.

Note 9.—Fritsch (1908) interpreted the enigmatic Ordovician fossil *Furca bohemica* as a crinoid pluteus larva, but it was later shown to be a marellamorph (Arthropoda) (Perner 1919, Mortensen 1921:233, Prokop 1989:143–144). Echinopluteus skeletal rods and baskets were described by Deflandre-Rigaud (1946) from the Upper Jurassic of France. Emlet (1985) has shown that the crystallographic orientation of ocular and genital plates in echinoids is a reliable indicator either of indirect development with an echinopluteus (certain of these plates growing from the larval spicules of the echinopluteus) or of direct development without a pluteus (these plates then being formed de novo); he has used this technique to determine the mode of development of fossil echinoids.

Note 10.—The use by Smith (1984a) and Paul & Smith (1984) of the pluteus larva as a synapomorphy between ophiuroids and echinoids has been questioned by Smith (1984b:452–453). He concluded that "There is therefore a distinct possibility that elongation of the small processes common to all eleutherozoan larvae occurred independently in ophiuroids and echinoids." Here I consider an alternative to the proposal of Paul & Smith (1984:469) that the larval type of Ordovician ophiuroids was an ophiopluteus.

Note 11.—To the best of my knowledge, a planktotrophic larval stage is still not known in the Phrynophiurida (Fell 1967: S71–S72, Patent 1970, Strathmann 1975, Hotchkiss 1978:542–543, Hendler 1991). More research on the development of the Phrynophiurida is needed. Dowidar & El-Maghraby (1970:260) listed in their plankton the ophiopluteus of *Ophiomyxa pentagona,* but did not provide any evidence to support this identification. It is therefore very important that the embryology and larval type of *Ophiomyxa pentagona,* and of other ophiomyxine and euryaline phrynophiurids be worked out. Knowledge of the development of *Ophiocanops* could be particularly rewarding because it is thought to have retained the gonadal and stomachal characters of the Oegophiurida (Fell 1963c: 481, Hotchkiss 1977, Petr 1988:38). The egg size of *Ophiocanops fugiens* was judged by Hendler (1975) to indicate direct or abbreviated development. [Concerning the classification of *O. fugiens*: It does not have the "auluroid" vertebrae of the Oegophiurida. The presence of oral and adoral shields, a first ventral arm plate, and streptospondyline vertebrae verify that *Ophiocanops* is a phrynophiurid (Mortensen 1933, Hotchkiss 1977). The extraordinary soft part characters support family rank and suggest (following Fell 1962) that *O. fugiens* may be a living representative of the stem group for the Order Phrynophiurida.] Hendler (1975) and Strathmann (1993) caution against inferences based on assuming that if a species has primitive features as an adult that its larval traits are also primitive. Strathmann also cautions (in litt.) that there is a weakness in parts of the inferences of Fell and Patent. He mentions as counter examples: that *Pteraster tesselatus* has no trace of bilateral larval symmetry yet it is descended from an ancestor with a brachiolaria (McEdward 1992); and that those species of *Ophiolepis, Ophioderma* and *Ophionereis* that lack any vestige of a larval skeleton in their vitellaria larvae are, nevertheless, descended from ancestors with an ophiopluteus (Strathmann 1988, 1993). [Hendler's (1982) studies on *Ophionereis annulata* and Mladenov's (1985) studies on *Ophiocoma pumila* have now demonstrated a connection between the ophiopluteus and the vitellaria.] As another counter example, Emlet informs me (in litt.) that he has studied the development of an *Amphiodia* with a benthic egg capsule and a direct development with no vestige of a larval skeleton. These comments emphasize the speculative nature of attempting to deduce the characteristics of ancestral ophiuroid larvae.

Note 12.—Jackson (1912:33) observed that "the first oculars to become insert are the plates of the bivium, next the plates of the posterior pair of the trivium, and last, if at all, the anterior odd plate of the trivium. . . . The ocular plates therefore in many regular Echini express a bilateral symmetry in this group, and an orientation passing through ambulacrum III and interambulacrum 5, the plane of symmetry adopted by Lovén." Jackson extended this correlation to plates of the oral surface (1927:556): "The law of sequence of incoming oculars in Echini indicates an arrangement to the right and left of the anteroposterior axis through III-5. This is in support of Lovén's law of the orderly arrangement of primordial ambulacral plates in clypeastroids, spatangoids, and young regular Echini, the Ia, IIa, IIIb, IVa, Vb are larger, while the Ib, IIb, IIIa, IVb, Va are smaller. So that from them as with a key one can gather the true orientation of an echinoid." Fell (*in* Moore & Fell 1966) added the insight that the insert condition of oculars I and V is the result of rearward migration of the anus toward interambulacrum 5, and that this rearward migration was already evident in the Cidaroida. [It is also noteworthy that Onoda (1933) showed a physiological anterior-posterior axis in *Heliocidaris* that coincides with the III-5 axis of Lovén's plane.]

Note 13.—A close relation between echinoids and asterozoans, based on study of *Palaeodiscus, Aulechinus* and *Ectinechinus,* was proposed by Spencer (1904), Bather & Spencer (1934), and MacBride & Spencer (1938). Evidence for a close relation between echinoids and ophiuroids was developed in detail by Hyman (1955:699) and most recently by Smith (1984a). Smith's cladogram accounts for the similarity of the adult morphologies of asteroids and ophiuroids, and the (apparent) similarity of the larval morphologies of ophiuroids and echinoids, by showing the stem ophiuroid as most closely related to the asteroids, and the stem echinoid as most closely related to the ophiuroids. However, with the similarity of the larvae now reappraised as a homeomorphism, with Lovén's law comprehended as an ancestral character that was present in the edrioasteroids (symplesiomorphy), and with a new table of ray homologies showing numerous changes in the location of the madreporite, the cladogram of Smith is in need of revision.

As stated by Mooi (1989) it is the "interpretations of the homologies of characters deemed important" that will determine the resulting cladogram, and not the actual use of cladistic methods. I accept the conclusions of Fell (1963b, 1963c) that ophiuroids display vestiges of metapinnular structure; that ophiuroids therefore derive from somasteroids (which have metapinnules); and that echinoids derive from a stock with meridional growth gradients that did not have metapinnules. Therefore, I agree with Fell that ophiuroids do not qualify as ancestors to the echinoids. I agree with Fell that the Asterozoa and the Echinozoa are ancient and independent lineages, and I disagree with Smith's (1984b) combining ophiuroids with echinoids and holothurians in a new Superclass Cryptosyringida. [A recent study on mitochondrial gene arrangements supports grouping asteroids with ophiuroids into the Asterozoa, and grouping echinoids with holothurians into the Echinozoa (Smith et al. 1993).] I interpret the fact of sharing Lovén's law to mean that ophiuroids and echinoids belong to the same 2-1-2 clade as the edrioasteroids. Thus I agree with Smith's (1984b) reconstitution of the Subphylum Eleutherozoa, which he expands to include stromatocystitoid and other edrioasteroids.

Note 14.—The probability under the null hypothesis H0 that a out of n arms will have a specific character state (the A or the B that is needed to spell out Lovén's law) is given by the binomial distribution with $p = q = 0.5$. The probability of observing a or more of the specific character in a sample of n observations has been calculated for each of the data on arms in Table 7 [exact calculations under the null hypothesis].

Arm I: $P(a \geq 9, n = 9) = 1/512$

Arm II: $P(a \geq 10, n = 13) = 378/8192$

Arm III: $P(a \geq 12, n = 12) = 1/4096$

Arm IV: $P(a \geq 10, n = 11) = 12/2048$

Arm V: $P(a \geq 6, n = 8) = 37/256.$

Using a criterion of $P<0.05$, the null hypothesis is rejected for arms I, II, III and IV. Although the null hypothesis could not be rejected for arm V, undoubtedly that will change when more Set II observations become available. The working hypothesis that each arm position relative to the madreporite has a preferred character state, that the preferred character states spell out Lovén's law, and that this pattern identifies the madreporic interradius as III/IV is supported.

The working hypothesis does not assume that any subset of rays is more (or less) faithful to its predominant character state than any other subset. This allows pooling the 53 observations of Set II and the 60 observations of Set I. The number of ocurrences of the predominant character state is $a = 107$ in $n = 113$ observations. The observed frequency is therefore 0.947. The probability that a specimen will have the predominant character state in all five of its arms, and therefore spell out Lovén's law, is $(0.947)^5 = 0.762$. In my previous study (Hotchkiss 1978) I reported an estimated observed frequency of 0.617 [with a 0.99 confidence interval on the estimate spanning from 0.33 to 0.85].

Conference paper.—Portions of this paper were presented at the second North American Friends of Echinoderms confer-

ence and workshop at the Harbor Branch Oceanographic Institution, Inc., 9–11 July 1992, with the title "Footnotes on Lovén's law". In the excellent atmosphere of discussions among the scientists at the meeting, I learned from Dr. Richard Mooi that he and Dr. Bruno David had also discovered that Lovén's law applies to *Stromatocystites walcotti,* and that they had used Smith's published drawings is exactly the same way as I report here. Further, Dr. Mooi informed me that he concurs with the characterization of Lovén's law in echinoids as a recapitulation of the 2-1-2 organization of *Camptostroma* and the edrioasteroids.

Acknowledgments

I thank David L. Pawson for constant help for over 25 years, without which I would not have been able to do this or any other research on echinoderms. I thank Anita P. Hotchkiss, David L. Pawson, Václav Petr, Richard Strathmann, Richard Emlet, and Gordon Hendler for reading and commenting on drafts of this manuscript. I thank Andrew Smith for his stimulating papers, his extremely important and exact observations on *Stromatocystites,* and for correspondence on the subject of situs inversus; Peter A. Jell for help with photographs and observations on ophiuroids used in the Appendix, and for reprints and his extremely important and exact observations on *Gillocystis.* I thank S. K. Donovan and an anonymous reviewer for their helpful reviews. I thank S. K. Donovan for informing me of the suggestion by Conway Morris (1993) that *Echmatocrinus* is actually a coelenterate and not a crinoid. I thank J. Sprinkle for a verbal communication confirming that *Echmatocrinus* has plates and reaffirming his opinion that it is a crinoid and not a coelenterate. I thank Gordon Hendler for informing me of the bilateral symmetry in *Asteronyx* and of the paper by Muus (1981), and for general communications and encouragement over many years; Richard Emlet for correspondence on the relation of the larva to the adult in echinoids and for reprints; Richard Strathmann for his willing responses to my phone calls for help; Jon W. Branstrattor for correspondence, reprints and advice on locating specimens for this study; David L. Meyer for being a willing host during my visits to the University of Cincinnati; Richard Terry of the University of Cincinnati for showing me material that he collected; W. Bruce Gibson of Cincinnati, Ohio, Thomas Frushour of Temperance, Michigan, and Kevin Brett of West Hill, Ontario, for allowing me to examine Ordovician ophiuroid materials; Janet Waddington, Peter von Bitter and Desmond Collins for their kind reception and help during my visit to the Royal Ontario Museum; Greg Buckley for help during visits to the Chicago Field Museum; H. C. Klinger of the South African Museum and J. E. Almond of the S. A. Geological Survey for information on Bokkeveld ophiuroids under study by P. A. Jell; John Harper, J. Roman and E. P. F. Rose for correspondence and reprints; Václav Petr for his generous help through correspondence, latex casts of specimens, papers (including translating the paper by Perner on *Furca,* and for additional references on *Furca*); Kraig Derstler for latex casts of material in the North Museum at Franklin and Marshall College; Niles Eldredge and Melvin T. Hinkley for assistance with the collections at the American Museum of Natural History; Ivo Chlupac for information and references on *Furca bohemica*; David N. Lewis for latex casts of BM(NH) material; Christina Franzén-Bengtson for information on the anal cone in the Gotland ophiuroid; the Boxboro Library for introducing me to Polya's (1954) book on plausible inference; James Doherty and Alan Doherty for their expert help in preparing rubber casts for this study; Donna Nordberg for help in final preparation of the manuscript; Rita Vine for help in obtaining the copyright permissions for the figures. I thank Dan Blake, John Dearborn, Lee Ehrman, Julian Fell, Anita P. Hotchkiss, Grace M. Hotchkiss, Peter Jell, Caleb Kaufman, John Lawrence, David Pawson, Ira B. Perelle, Václav Petr and Richard Strathmann for help with literature. I thank: The Paleontological Society for permission to use Text. Figs. 1 & 2 of Hotchkiss 1978 as the basis for Figs. 1 & 2 herein; Cambridge University Press for permission to use Fig. 6 of Bather 1914b as the basis for Fig. 3; A. B. Smith and Cambridge University Press for permission to use Fig. 7 of Paul & Smith 1984 as the basis for Fig. 4; P. A. Jell and the Association of Australasian Palaeontologists for permission to use Fig. 14 of Jell 1983 as the basis for Fig. 5; D. L. Pawson for providing the final preparation of the figures.

Dedication

This paper is dedicated in memory of Prof. H. Barraclough Fell (1917–1994), whom I cherished as mentor and friend. Fell's enthusiasm and charisma, and the sincerity and collegiality with which he treated his young students (as experienced by James F. Clark and myself in the 1960s) made him one of the most important influences in my life, both personally and scientifically. I believe that these remarks would be readily echoed by his other students. To prepare this manuscript I reread papers by Fell that had ignited my interest in echinoderms while an undergraduate student. Part of the pleasure and the challenge of writing this paper has been to try to do justice to the seminal ideas of this great scholar. Thus, in the section of this paper where I discuss the ophiopluteus, an additional goal is to provide access to Fell's treatment of the topic by giving detailed page references.

Literature Cited

Baranova, Z. I. 1982. Occurrence of the sea-urchin of the tropical family Temnopleuridae off the Paramushir Island.—Academy of Sciences of the USSR, Zoological Institute, Explorations of the Fauna of the Seas 29(37) Marine Invertebrates of Coastal Biocenoses of the Arctic Ocean and the Pacific Ocean: 114–118.

Bather, F. A. 1900a. General description of the Echinoderma. Pp. 1–37 *in* E. R. Lankester, ed., A treatise on zoology, part III, the Echinoderma. Adam & Charles Black, 344 pp.

———. 1900b. The Edrioasteroidea. Pp. 205–216 *in* E. R. Lankester, ed., A treatise on zoology, part III, the Echinoderma. Adam & Charles Black, 344 pp.

———. 1914a. Studies in Edrioasteroidea. IV. The edrioasters of the Trenton Limestone [part I].—Geological Magazine, new series, decade VI, 1:115–125, pls. 10–12.

———. 1914b. Studies in Edrioasteroidea. V. *Steganoblastus.*—Geological Magazine, new series, decade VI, 1:193–203, pl. 15.

———. 1915. Studies in Edrioasteroidea. IX. The genetic relations to other echinoderms.—Geological Magazine, new series, decade VI, 2:393–403.

———, & W. K. Spencer. 1934. A new Ordovician echinoid from Girvan, Ayreshire.—Annals and Magazine of Natural History, ser. 10, 13:557–558.

Beer, G. R. de. 1940. Embryology and taxonomy. Pp. 365–393 *in* J. Huxley, ed., The new systematics. Oxford University Press, London. 583 pp.

Bell, B. M. 1976a. A study of North American Edrioasteroidea.—Memoir 21 of the New York State Museum and Science Service, Albany, NY, 447 pp.

———. 1976b. Phylogenetic implications of ontogenetic development in the Class Edrioasteroidea (Echinodermata).—Journal of Paleontology 50:1001–1019.

Blake, D. B. 1987. A classification and phylogeny of post-Palaeozoic sea stars (Asteroidea: Echinodermata).—Journal of Natural History 21:481–528.

———. 1988. Paxillosidans are not primitive asteroids: a hypothesis based on functional considerations. Pp. 309–314 *in* R. D. Burke, P. V. Mladenov, P. Lambert, & R. Parsley, eds., Echinoderm biology: proceedings of the Sixth International Echinoderm Conference, Victoria, 23–28 August 1987. A. A. Balkema, Rotterdam, Netherlands, 818 pp.

———, & T. E. Guensburg. 1989. Two new multiarmed Paleozoic (Mississippian) asteroids (Echinodermata) and some paleobiologic implications.—Journal of Paleontology 63:331–340.

———, & ———. 1993. New Lower and Middle Ordovician stelleroids (Echinodermata) and their bearing on the origins and early history of the stelleroid echinoderms.—Journal of Paleontology 67:103–113.

Branstrator, J. W. 1972. *Lanthanaster cruciformis,* a new Upper Ordovician sea star from Cincinnati, Ohio.—Journal of Paleontology 46:66–69.

———. 1979. Asteroidea (Echinodermata). Paper 1066-F [Pp. F1–F7 + pls. 1–3] *in* John Pojeta, ed., Contributions to the Ordovician paleontology of Kentucky and nearby states.—U.S. Geological Survey Professional Paper 1066-A-G.

Brooks, W. K., & C. Grave. 1899. Ophiura brevispina.—Memoirs of the National Academy of Sciences 8:79–100 + pls. 1–3.

Brower, J. C. 1985. Ontogeny and functional morphology of two Ordovician calceocrinids. Pp. 13–18 *in* B. F. Keegan & B. D. S. O'Connor, eds., Echinodermata: proceedings of the Fifth International Echinoderm Conference, Galway, 24–29 September 1984. A. A. Balkema, Rotterdam, Netherlands, 662 pp.

Bury, H. 1889. Studies in the embryology of the echinoderms.—Quarterly Journal of Microscopical Science, new series 29:409–447 + pls. 37–39.

Caster, K. E. 1967. Homoistela. Pp. S581–S627 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, Part S, Echinodermata 1, volume 2. The Geological Society of America and The University of Kansas Press, S297–S650 pp.

Chadwick, H. C. 1923. Asterias.—Liverpool Marine Biology Committee Memoirs on Typical British Marine Plants and Animals 25:1–63 + pls. 1–9.

Chesnut, D. R., & F. R. Ettensohn. 1988. Hombergian (Chesterian) echinoderm paleontology and paleoecology, south-central Kentucky.—Bulletins of American Paleontology 95(330):1–102 + table 6.

Clark, A. M. 1977. Starfishes and related echinoderms. Third edition. T.F.H. Publications, Inc., Ltd. 160 pp. [Originally published as Starfishes and their relations, first edition 1962, British Museum (Natural History).]

———, & J. Courtman-Stock. 1976. The echinoderms of southern Africa. British Museum (Natural History), 277 pp. [British Museum (Natural History) Publication No. 776.]

Clark, H. L. 1921. The echinoderm fauna of Torres Strait: its composition and its origin.—Department of Marine Biology of The Carnegie Institution of Washington 10:1–223 + 38 pls. [Carnegie Institution of Washington Publication No. 214.]

Clark, W. B., & M. W. Twitchell. 1915. The Mesozoic and Cenozoic Echinodermata of the United States.—Monographs of the United States Geological Survey 54:1–341.

Conway Morris, S. 1993. The fossil record and the early evolution of the Metazoa.—Nature 361: 219–225.

Deflandre-Rigaud, M. 1946. Vestiges microscopiques des larves d'Échinodermes de l'Oxfordian de Villers-sur-Mer.—Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences 222:908–910.

Derstler, K. L. 1985. Studies on the morphological evolution of echinoderms. Unpublished Ph.D. dissertation, University of California, Davis, University Microfilms International, 438 pp.—Dissertation Abstracts International 46:2238B.

Donovan, S. K. 1992. Scanning EM study of the living cyrtocrinid *Holopus rangii* (Echinodermata, Crinoidea) and implications for its functional morphology.—Journal of Paleontology 66: 665–675.

Dowidar, N. M., & A. M. El-Maghraby. 1970. The neritic zooplankton of the south eastern Mediterranean at Alexandria. I. Distribution and ecology of the zooplankton organisms with special reference to Copepoda.—United Arab Republic, Ministry of Scientific Research, Bulletin of the Institute of Oceanography and Fisheries 1:225–273.

Durham, J. W. 1966. Classification [of echinozoans]. Pp. U270–U297 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, Part U, Echinodermata 3, volume 1. The Geological Society of America and The University of Kansas Press, 366 pp.

Emlet, R. B. 1985. Crystal axes in Recent and fossil adult echinoids indicate trophic mode in larval development.—Science 230:937–940.

———. 1988. Crystallographic axes of echinoid genital plates reflect larval form: some phylogenetic implications. Pp. 299–310 (chapter 23) *in* C. R. C. Paul & A. B. Smith, eds., Echinoderm phylogeny and evolutionary biology. Clarendon Press, Oxford, 373 pp.

———. 1989. Apical skeletons of sea urchins (Echinodermata: Echinoidea): two methods for inferring mode of larval development.—Paleobiology 15:223–254.

Fay, R. O. 1967. Edrioblastoids. Pp. S289–S292 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, Part S, Echinodermata 1, volume 1. The Geological Society of America and The University of Kansas Press, 296 pp.

Fell, H. B. 1941a. The direct development of a New Zealand ophiuroid.—Quarterly Journal of Microscopical Science 82:377–441 + pls. 20–22.

———. 1941b. Probable direct development in some New Zealand ophiuroids.—Transactions and Proceedings of the Royal Society of New Zealand 71:25–26.

———. 1945. A revision of the current theory of echinoderm embryology.—Transactions of the Royal Society of New Zealand 75:73–101.

———. 1946. The embryology of the viviparous ophiuroid *Amphipholis squamata* Delle Chiaje.—Transactions of the Royal Society of New Zealand 75:419–464.

———. 1948. Echinoderm embryology and the origin of chordates.—Biological Reviews 23:81–107.

———. 1962. Evidence for the validity of Matsumoto's classification of the Ophiuroidea.—Publications of the Seto Marine Biological Laboratory 10:145–152.

———. 1963a. A new family and genus of Somasteroidea.—Transactions of the Royal Society of New Zealand (Zoology) 3:143–146.

———. 1963b. The phylogeny of sea-stars.—Philosophical Transactions of the Royal Society of London, Series B, 246:381–435 + pls. 50–51.

———. 1963c. The evolution of the echinoderms.—Annual Report Smithsonian Institution 1962: 457–490.

———. 1965. The early evolution of the Echinozoa.—Breviora 219:1–17.

———. 1966a. Ancient echinoderms in modern seas.—Oceanography and Marine Biology Annual Review 4:233–245.

———. 1966b. The ecology of ophiuroids. Chapter 6, pp. 129–143 *in* R. A. Boolootian, ed., Physiology of Echinodermata. Interscience Publishers, New York, 822 pp.

———. 1967. Echinoderm ontogeny. Pp. S60–S85 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, Part S, Echinodermata 1, volume 1. The Geological Society of America and The University of Kansas Press, 296 pp.

———, & D. L. Pawson. 1966. Echinacea. Pp. U367–U440 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, Part U, Echinodermata 3, volume 2. The Geological Society of America and The University of Kansas Press, U367–U695 pp.

Franzén, C. 1979. Echinoderms. Pp. 216–224 *in* Valdar Jaanusson, Sven Laufeld and Roland Skoglund, eds., Lower Wenlock faunal and floral dynamics—Vattenfallet Section, Gotland.—Sveriges Geologiska Undersökning, serie C nr 762, Avhandlingar och Uppsatser, Årsbok 73 nr 3. 296 pp.

Fritsch, Ant. 1908. Über eine Echinodermenlarve aus dem Untersilur Böhmens.—Zoologischer Anzeiger 33:797–798.

Fujita, T., & S. Ohta. 1988. Photographic observations of the life style of a deep-sea ophiuroid *Asteronyx loveni* (Echinodermata).—Deep-Sea Research 35:2029–2034.

Gemmill, J. F. 1914. The development and certain points in the adult structure of the starfish *Asterias rubens*, L.—Philosophical Transactions of the Royal Society of London, series B, 205:213–294 + pls. 18–24.

Gordon, I. 1929. Skeletal development in *Arbacia, Echinarachnius* and *Leptasterias.*—Philosophical Transactions of the Royal Society of London, series B, 217:289–334.

Grabowsky, G. L. 1994. Symmetry, locomotion and the evolution of an anterior end: A lesson from sea urchins.–Evolution 48:1130–1146.

Gray, I. E., M. E. Downey & M. J. Cerame-Vivas. 1968. Sea-stars of North Carolina.—U.S. Fish and Wildlife Service Fishery Bulletin 67:127–163.

Hahn, G., & C. Brauckmann. 1981. Ein neuer Ophiuren-Fund aus dem Kulm von Herborn (Asterozoa, Unter-Karbon IIIα, Hessen).—Geologisches Jahrbuch Hessen 109:5–18.

Hammann, W., & S. Schmincke. 1986. Depositional environment and systematics of a new ophiuroid, *Taeniaster ibericus* n. sp., from the Middle Ordovician of Spain.—Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen. 173:47–74.

Hansman, R. H., F. C. Shaw, & W. A. Pettyjohn. 1962. Supplement to the catalog of the type specimens of fossils in the University of Cincinnati Museum. University of Cincinnati, Cincinnati, 131 pp.

Harper, J. A. 1985. A new look at *Eugasterella logani* (Hall, 1868) (Stelleroidea: Ophiuroidea) from the Middle Devonian of New York State.—Annals of the Carnegie Museum 54:357–373.

———, & R. W. Morris. 1978. A new encrinasterid ophiuroid from the Conemaugh Group (Pennsylvanian) of western Pennsylvania, and revision of the Encrinasteridae.—Journal of Paleontology 52:155–163.

Haude, R. 1982. Ophiuren (Echinodermata) aus dem Karbon des Rheinischen Schiefergebirges.—Geologisches Jahrbuch Hessen 110:5–25.

———. 1994. Fossil holothurians: constructional morphology of the sea cucumber, and the origin of the calcareous ring. Pp. 517–522 *in* B. David, A. Guille, J. P. Feral, & M. Roux, eds., Echinoderms through time: proceedings of the eighth international echinoderm conference, Dijon, 6–10 Sept. 1993. A. A. Balkema, Rotterdam, Netherlands, 940 pp.

———, & F. Langenstrassen. 1976. *Rotasaccus dentifer* n.g.n. sp., ein devonischer Ophiocistioide (Echinodermata) mit "holothuroiden" Wandskleriten und "echinoidem" Kauapparat.—Paläontologische Zeitschrift 50:130–150.

Hawkins, H. L., & S. M. Hampton. 1927. The occurrence, structure, and affinities of *Echinocystis* and *Palaeodiscus.*—Quarterly Journal of the Geological Society of London 83:574–603, pls. 44–46.

Hendler, G. 1975. Adaptational significance of the patterns of ophiuroid development.—American Zoologist 15:691–715.

———. 1982. An echinoderm vitellaria with a bilateral larval skeleton: evidence for the evolution of ophiuroid vitellariae from ophioplutei.—Biological Bulletin of the Marine Biology Laboratory, Woods Hole 163:431–437.

———. 1991. Echinodermata: Ophiuroidea. Chapter 6, pp. 355–511 *in* A. C. Giese, J. S. Pearse, & V. B. Pearse, eds., Reproduction of marine invertebrates, vol. VI, echinoderms and lophophorates, The Boxwood Press, Pacific Grove, California, 808 pp.

Hotchkiss, F. H. C. 1970. North American Ordovician Ophiuroidea—the genus *Taeniaster* Billings, 1858 (Protasteridae).—Proceedings of the Biological Society of Washington 83:59–76.

———. 1977. Ophiuroid *Ophiocanops* (Echinodermata) not a living fossil.—Journal of Natural History 11:377–380.

———. 1978. Studies on echinoderm ray homologies: Lovén's law applies to Paleozoic ophiuroids.—Journal of Paleontology 52:537–544.

———. 1979. Case studies in the teratology of starfish.—Proceedings of the Academy of Natural Sciences of Philadelphia 131:139–157.

———. 1980. The early growth stage of a Devonian ophiuroid and its bearing on echinoderm phylogeny.—Journal of Natural History 14:91–96.

———. 1993. A new Devonian ophiuroid (Echinodermata: Oegophiurida) from New York State and its bearing on the origin of ophiuroid upper arm plates.—Proceedings of the Biological Society of Washington 106:63–84.

———, & P. R. Seegers. 1976. Variable symmetry in starfish.—Thalassia Jugoslavica 12(1):173–180.

Hyman, L. H. 1955. The Invertebrates: Echinodermata. Volume IV. McGraw-Hill, New York, 763 pp.

Irimura, S. 1991. Ophiuroidea. Pp. 111–152 *in* C. Oguro and T. Okutani, eds., Echinoderms from continental shelf and slope around Japan, Vol. II. Japan Fisheries Resource Conservation Association, Tokyo, 204 pp.

Jackson, R. T. 1899. Localized stages in development in plants and animals.—Memoirs of the Boston Society of Natural History 5:89–153 + pls. 16–25.

———. 1903. Localized stages in the development of plants and animals [paper summary].—Annals of the New York Academy of Sciences 15: 80–81.

———. 1912. Phylogeny of the Echini, with a revision of Palaeozoic species.—Memoirs of the Boston Society of Natural History 7:1–491 + pls. 1–76.

———. 1927. Studies of *Arbacia punctulata* and allies, and of nonpentamerous Echini.—Memoirs of the Boston Society of Natural History 8:437–565.

———. 1929. The status of Bothriocidaris.—Bulletin of the Museum of Comparative Zoology at Harvard College 69:481–512.

Jell, P. A. 1983. Early Devonian echinoderms from Victoria (Rhombifera, Blastoidea and Ophiocistioidea). Pp. 209–235 *in* J. Roberts & P. A. Jell, eds., Memoir 1. T. Dorothy Hill jubilee memoir: proceedings of a meeting organized by the Association of Australasian Palaeontologists at the University of Queensland, 9th and 10th September 1982. Association of Australasian Palaeontologists, Sydney, 371 pp.

Kesling, R. V. 1962. Notes on *Protopalaeaster narrawayi* Hudson.—Journal of Paleontology 36: 933–942 + pls. 133–134.

———. 1969. A new brittle-star from the Middle Devonian Arkona shale of Ontario.—Contributions from the Museum of Paleontology, The University of Michigan (Ann Arbor) 23:37–51.

———, & D. Le Vasseur. 1971. *Strataster ohioensis,* a new Early Mississippian brittle-star, and the paleoecology of its community.—Contributions from the Museum of Paleontology, The University of Michigan (Ann Arbor) 23:305–341.

———, & H. L. Strimple. 1966. *Calliasterella americana,* a new starfish from the Pennsylvanian of Illinois.—Journal of Paleontology 40:1157–1166 + pls. 151–153.

Kier, P. M. 1965. Evolutionary trends in Paleozoic echinoids.—Journal of Paleontology 39:436–465.

———. 1968. Echinoids from the Middle Eocene Lake City Formation of Georgia.—Smithsonian Miscellaneous Collections 153(2):1–45.

Kilfoyle, C. F. 1954. Catalog of type specimens of fossils in the New York State Museum. Supplement 4.—New York State Museum Bulletin 348: 1–719.

Lane, N. G., & G. D. Webster. 1967. Symmetry planes of Paleozoic crinoids.—The University of Kansas Paleontological Contributions 25:14–16.

Lewis, D. N. 1993. Catalogue of the type and figured specimens of fossil Asteroidea and Ophiuroidea in The Natural History Museum.—Bulletin of The Natural History Museum (Geology) 49:47–80.

Lorenz, K. Z. 1974. Analogy as a source of knowledge.—Science 185:229–234.

Lovén, S. 1874. Études sur les echinoidées.—Kongelige Svenska Vetenskaps-Akademiens Handlingar (n. ser.) 11(7):1–91 + pls. 1–53.

Lütken, C. F., & Th. Mortensen. 1899. The Ophiuridae. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer

"Albatross," during 1891, Lieut. Commander Z. L. Tanner, U.S.N., commanding.—Memoirs of the Museum of Comparative Zoology at Harvard College 23(2):1–208 + 23 pls.

MacBride, E. W., & W. K. Spencer. 1938. Two new Echinoidea, *Aulechinus* and *Ectinechinus*, and an adult plated holothurian, *Eothuria*, from the Upper Ordovician of Girvan, Scotland.—Philosophical Transactions of the Royal Society of London, series B, 229:91–136 + pls. 10–17.

Macurda, D. B. 1964. The blastoid *Pentremites* Say—a trimerous mutant and some new occurrences.—Journal of Paleontology 38:705–710.

———. 1978. Abnormalities and asymmetries in blastoids—a key to larval bilateral symmetry?.—Geological Society of America Abstracts with Programs 10:449.

———. 1980. Abnormalities of the Carboniferous blastoid *Pentremites*.—Journal of Paleontology 54:1155–1162.

McEdward, L. R. 1992. Morphology and development of a unique type of pelagic larva in the starfish *Pteraster tesselatus* (Echinodermata: Asteroidea).—Biological Bulletin of the Marine Biology Laboratory, Woods Hole 182:177–187.

McIver, M. A., & E. P. McIver. 1955. 300-million-year-old starfishes.—Natural History (Magazine of the American Museum of Natural History) 64:159.

Melville, R. V., & J. W. Durham. 1966. Skeletal morphology. Pp. U220–U257 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, Part U, Echinodermata 3, volume 1. The Geological Society of America and The University of Kansas Press, 366 pp.

Mladenov, P. V. 1985. Development and metamorphosis of the brittle star *Ophiocomina pumila*: evolutionary and ecological implications.—Biological Bulletin of the Marine Biology Laboratory, Woods Hole 168:285–295.

Mooi, R. 1989. Evolutionary dissent.—Paleobiology 15:437–444.

Moore, R. C., & H. B. Fell. 1966. Homology of echinozoan rays. Pp. U119–U131 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, Part U, Echinodermata 3, volume 1. The Geological Society of America and The University of Kansas Press, 366 pp.

Mortensen, Th. 1921. Studies of the development and larval forms of echinoderms. G. E. C. Gad, Copenhagen. 261 pp. + 33 pls.

———. 1928. Bothriocidaris and the origin of echinoids.—Videnskabelige Meddelelser fra Dansk naturhistorisk forening i København 86:93–122.

———. 1930. Bothriocidaris and the ancestry of echinoids. A reply.—Videnskabelige Meddelelser fra Dansk naturhistorisk forening i København 90: 313–352.

———. 1933. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916. LX. On an extraordinary Ophiurid, Ophiocanops fugiens Koehler. With remarks on Astrogymnotes, Ophiopteron, and on an albino Ophiocoma.—Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København 93:1–21 + pl. 1.

Muus, K. 1981. Density and growth of juvenile *Amphiura filiformis* (Ophiuroidea) in the Øresund.—Ophelia 20:153–168.

Onoda, K. 1931. Notes on the development of Heliocidaris crassispina with special reference to the structure of the larval body.—Memoirs of the College of Science, Kyoto Imperial University, Series B, 7:103–134, pls. 5–7.

———. 1933. On the orientation of the regular sea-urchin Heliocidaris crassispina.—Japanese Journal of Zoology 5:159–164.

Owen, H. G. 1965. The British Palaeozoic Asterozoa. Table of contents, supplement and index:i-vii + 541-583.—Palaeontographical Society (London) volume for 1964.

Parks, W. A. 1908. Notes on the ophiuran genus Protaster, with description of a new species.—Transactions of the Canadian Institute 8:363–372.

Patent, D. 1970. The early embryology of the basket star *Gorgonocephalus caryi* (Echinodermata, Ophiuroidea).—Marine Biology 6:262–267.

Paul, C. R. C., & A. B. Smith. 1984. The early radiation and phylogeny of echinoderms.—Biological Reviews 59:443–481.

Pawson, D. L. 1971. *Ekkentropelma brychia* n. g., n. sp., an Antarctic psolid holothurian with a functionally lateral sole.—Proceedings of the Biological Society of Washington 84:113–118.

Perner, J. 1919. Furca bohemica—zástupce nové čeledi korýšů v českém siluru.—Casopsis Musea Království Ceského 93:32–33.

Petr, Václav. 1988. A notice on the occurrence of *Bohemura jahni* Jaekel, 1903 (Echinodermata, Ophiuroidea) in the Bohemian Middle Ordovician.—Věstník Ústředního ústavu geologického 63:35–38 + pls. I-IV.

———. 1989. Revision of morphology and ecology of *Bohemura jahni* Jaekel, 1903 (Ophiuroidea, Protasteridae) from Bohemian Middle Ordovician.—Sborník Národního Muzea v Praze (Acta Musei Nationalis Pragae), series B—historie naturalis, 45:1–20 + pls. I–VIII.

Polya, G. 1954. Patterns of plausible inference. [volume II of Mathematics and plausible reasoning.] Princeton University Press, 190 pp.

Prokop, Rudolf. 1989. Zkamenělý svět. Kotva, Prague. 275 pp.

Regnéll, G. 1966. Edrioasteroids. Pp. U136–U173 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, Part U, Echinodermata 3, volume

1. The Geological Society of America and The University of Kansas Press, 366 pp.

———. 1973. Tidiga tagghudingar.—Fauna och Flora 4:161–165. (Stockholm).

Roman, J. 1957. Les dyssymétries des *Echinolampas* fossiles (Échinides exocycles cassiduloïdes).—Bulletin de la Societé Géologique de France, 6th series 7:67–82.

Rose, E. P. F. 1976. Some observations on the Recent holectypoid echinoid *Echinoneus cyclostomus* and their palaeoecological significance.—Thalassia Jugoslavica 12(1):299–306.

Ruedemann, R. 1916. Account of some new or little-known species of fossils (Paleontologic contributions from the New York State Museum).—New York State Museum Bulletin 189:7–97 + pls. 1–31.

Schuchert, C. 1915. Revision of Paleozoic Stelleroidea with special reference to North American Asteroidea.—United States National Museum Bulletin 88:1–311 + pls. 1–38.

Smith, A. B. 1984a. Echinoid palaeobiology. [book series "Special topics in palaeontology": 1] George Allen & Unwin, London, 190 pp. + Fig. A.1.

———. 1984b. Classification of the Echinodermata.—Palaeontology 27:431–459.

———. 1985. Cambrian eleutherozoan echinoderms and the early diversification of edrioasteroids.—Palaeontology 28:715–756 + pls. 87–89.

———. 1988a. Fossil evidence for the relationships of extinct echinoderm classes and their times of divergence. Pp. 85–97 *in* C. R. C. Paul & A. B. Smith, eds., Echinoderm phylogeny and evolutionary biology. Published for the Liverpool Geological Society by Clarendon Press, Oxford, 373 pp.

———. 1988b. Patterns of diversification and extinction in early Palaeozoic echinoderms.—Palaeontology 31:799–828.

———, & M. A. Arbizu. 1987. Inverse larval development in a Devonian edrioasteroid from Spain and the phylogeny of Agelacrinitinae.—Lethaia 20:49–62.

———, & P. A. Jell. 1990. Cambrian edrioasteroids from Australia and the origin of starfishes.—Memoirs of the Queensland Museum 28:715–778.

Smith, J. E. 1950. Some observations on the nervous mechanisms underlying the behaviour of starfishes. Pp. 196–220 *in* Symposia of the Society for Experimental Biology, no. IV, Physiological Mechanisms in Animal Behaviour, Academic Press, New York, 482 pp.

Smith, M. J., A. Arndt, S. Gorski, & E. Fajber. 1993. The phylogeny of echinoderm classes based on mitochondrial gene arrangements.—Journal of Molecular Evolution 36:545–554.

Sollas, I. B. J., & W. J. Sollas. 1912. Lapworthura: a typical brittlestar of Silurian Age; with suggestions for a new classification of the Ophiuroidea.—Philosophical Transactions of the Royal Society of London, series B, 202:213–232 + pls. 9–10.

Spencer, W. K. 1904. On the structure and affinities of Palaeodiscus and Agelacrinus.—Proceedings of the Royal Society of London 74:31–46.

———. 1914. A monograph of the British Palaeozoic Asterozoa. Part 1:1–56 + pl. 1.—Palaeontographical Society (London), volume for 1913.

———. 1916. A monograph of the British Palaeozoic Asterozoa. Part 2:57–108 + pls. 2-5.—Palaeontographical Society (London), volume for 1915.

———. 1922. A monograph of the British Palaeozoic Asterozoa. Part 5:197–236 + pls. 14-17.—Palaeontographical Society (London), volume for 1920.

———. 1925. A monograph of the British Palaeozoic Asterozoa. Part 6:237–324. + pls. 18-22.—Palaeontographical Society (London), volume for 1922.

———. 1927. A monograph of the British Palaeozoic Asterozoa. Part 7:325–388 + pls. 23-24.—Palaeontographical Society (London), volume for 1925.

———. 1930. A monograph of the British Palaeozoic Asterozoa. Part 8:389–436 + pls. 25–28.—Palaeontographical Society (London), volume for 1928.

———. 1934. A monograph of the British Palaeozoic Asterozoa. Part 9:437–494 + pls. 29–32.—Palaeontographical Society (London), volume for 1933.

———. 1951. Early Palaeozoic starfish.—Philosophical Transactions of the Royal Society of London, Series B, 235:87–129.

———, & C. W. Wright. 1966. Asterozoans. Pp. U4–U107 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, part U, Echinodermata 3, volume 1. The Geological Society of America and The University of Kansas Press, 366 pp.

Sprinkle, J. 1973. Morphology and evolution of blastozoan echinoderms.—Special Publication [The Museum of Comparative Zoology, Harvard University], 284 pp.

Strathmann, R. 1974. Introduction to function and adaptation in echinoderm larvae.—Thalassia Jugoslavica 10:321–339.

———. 1975. Larval feeding in echinoderms.—American Zooologist 15:717–730.

———. 1978. Progressive vacating of adaptive types during the Phanerozoic.—Evolution 32:907–914.

———. 1988. Larvae, phylogeny, and von Baer's law. Pp. 53–68 *in* C. R. C. Paul & A. B. Smith, eds., Echinoderm phylogeny and evolutionary biol-

Table 4.—Key for processing specimens into two mutually exclusive sets for the study of Lovén's law and the location of the madreporite in Paleozoic ophiuroids.

A.	Oral view	B
	Aboral view	Exclude
B.	Specimen has recognizable madreporite	C
	Madreporite not found	Exclude
C.	One or more arms scorable	D
	No arms scorable	Exclude
D.	Five arms scorable	E
	One to four scorable arms	Set II
E.	Five arms conform to Lovén's law	Set I
	Five arms do not conform	Set II

ogy. Published for the Liverpool Geological Society by Clarendon Press, Oxford 373 pp.

———. 1993. Hypotheses on the origins of marine larvae.—Annual Review in Ecology and Systematics 24:89–117.

Swan, E. F. 1966. Growth, autotomy, and regeneration. Pp. 397–434 *in* R. A. Boolootian, ed., Physiology of Echinodermata. Interscience Publishers, New York, 822 pp.

Thoral, M. 1935. Contribution à l'étude paléontologique de l'Ordovicien inférieur de la Montagne Noire et révision sommaire de la faune Cambrienne de la Montagne Noire.—Thèses présentées à la Faculté des Sciences de l'Université de Paris, Série A, No. 1541 (No. d'ordre: 2407). Imprimerie de la Manufacture de la Charité, Montpellier. 362 pp.

Turner, R. L. 1974. Post-metamorphic growth of the arms in *Ophiophragmus filograneus* (Echinodermata: Ophiuroidea) from Tampa Bay, Florida (USA).—Marine Biology 24:273–277.

Übisch, L. von. 1913. Die Anlage und Ausbildung des skeletsystems einiger Echiniden und die Symmetrieverhältnisse von Larvae und Imago.—Zeitschrift für Wissenschaftliche Zoologie (Leipzig) 104:119–156 + pls. 6–7.

———. 1927. Über die Symmetrieverhältnisse von Larven und Imago bei regulären und irregulären Seeigeln.—Zeitschrift für Wissenschaftliche Zoologie (Leipzig) 129:541–566.

Waddington, J., P. H. von Bitter, & D. Collins. 1978. Catalogue of type invertebrate, plant, and trace fossils in the Royal Ontario Museum.—Life Sciences Miscellaneous Publications, Royal Ontario Museum, 151 pp.

Appendix I

Additional Data on Lovén's Law and the Location of the Madreporite in Ophiuroids

Methods.—Evidence of Lovén's law is obtained by recording the arrangement of the ambulacral plates (Hotchkiss 1978). Examined from the oral surface, the ambulacral series on the anticlockwise side of each arm is either in advance (A) or behind (B) the series on the clockwise side of the arm. The arrangement AABAB is Lovénian, and the labels I, II, III, IV, V apply to the arms (Fig. 2).

Two methods of analysis, based on mutually exclusive categories of specimens, provide separate looks at the location of the madreporite in connection with Lovén's law in Paleozoic ophiuroids. Specimens were processed into two sets following the dichotomous key given in Table 4.

The SET I collection of specimens all obey Lovén's law. Hence the arms can be labeled I, II, III, IV, V according to Lovén's system. The location of the madreporite is then determined by inspection to belong to a certain interradius by name, i.e., I/II, or II/III, etc. The working hypothesis is that the madreporite occurs almost exclusively in the III/IV interradius (Hotchkiss 1978). The null hypothesis is that there is no preferred location.

The SET II collection of specimens all have a madreporite. We will assign interradius designation III/IV to the madreporic interradius. Hence the arms can be labeled I, II, III, IV, V, according to their placement with respect to the madreporite. The character state of each scorable arm can be determined by inspection to be either "A" or "B." The working hypothesis is that each arm is associated with a particular character state and that the pattern conforms with Lovén's law. The null hypothesis is that there is no preferred character state for any arm.

Materials.—This study can use only those Paleozoic ophiuroids that have alternating ambulacral plates. The preservation must permit individual recognition of the 1st, 2nd, 3rd, etc., plates of each half series of ambulacral plates in order to score the character state. In some specimens the lateral plates of the two sides of the arm can be used to assist in the interpretation. To assist in proper scoring of the ambulacrals, it is necessary to prepare latex or silicone rubber casts of specimens preserved as molds. In some specimens the aboral view can be scored. In exceptional circumstances data can be taken from published photographs. It is fairly common for published drawings to contain reconstructed detail that would not be reliable for this study.

The specimens comprising Set I and Set II all belong to the families Protasteridae and Encrinasteridae, suborder Lysophiurina, order Oegophiurida.

Set I: Twelve specimens. Details are as follows:

101. *Protaster sedgwickii* Forbes, lectotype, Sedgwick Museum No. A6374, Lower Ludlow (Upper Silurian), Lake District, England (oral view; seen) (Hotchkiss 1978:specimen no. 1)

102. Protasteridae sp., North Museum, Franklin and Marshall College No. PE38, Devonian, from roadside near Portland, New York (oral view; seen) (Hotchkiss 1978:specimen no. 6)

103. Hamling's ophiuroid = Protasteridae sp. juv. British Museum (Natural History) No. E13737a, Upper Devonian, Pickard's Down, near Barnstaple, North Devon (oral view; seen) (Hotchkiss 1978:specimen no. 11; 1980:fig. 2B; Lewis 1993:69 as *Drepanaster scabrosus*)

104. *Stratаster ohioensis* Kesling & LeVasseur, paratype, University of Michigan Museum of Paleontology No. UMMP 58332a, Meadville Shale (Early Missippian), Cuyahoga County, Ohio (oral view; studied from the photograph: Kesling & LeVasseur 1971:pl. 7 fig. 4) (Hotchkiss 1978:542, 1993:65)

105. *Eugasterella logani* (Hall), Moscow Formation (Middle Devonian), near Earlville, Madison County, New York, the AAB*AB arm and madreporite arrangement reported by Harper (1985:367) is visible in his photograph of Carnegie Museum of Natural History No. CM 34422 (oral view; studied from the photograph: Harper 1985:fig. 7A) (The lateral plates help to score the arms.)

106. Protasteridae sp., South African Museum, Cape Town, SAM K1015 (formerly SAM 69d; originally from S.A. Geological Survey collections; plaster replica only), Gydo Formation (Devonian Bokkeveld Group), near Grootrivier, Cedarberg Mountains. (oral view; studied from photography supplied by Dr. P. A. Jell; under study by Dr. Jell; locality information from Dr. J. E. Almond) [an aged rubber pull of SAM 69d is in the Geology Museum of the University of Cincinnati]

107. Protasteridae sp., South African Museum, Cape Town, SAM K1014 (formerly SAM 203/67d; originally from S. A. Geological Survey collections), Gydo Formation (Devonian Bokkeveld Group), near Grootrivier, Cedarberg Mountains. (oral view; studied from photograph supplied by Dr. P. A. Jell; under study by Dr. Jell; locality information from Dr. J. E. Almond) [an aged rubber pull of SAM 203/67d is in the Geology Museum of the University of Cincinnati]

108–112. Protasteridae sp., Devonian Bokkeveld Group, South Africa. [oral views; studied from photographs loaned by Dr. P. A. Jell; material is under study by Dr. Jell; repository and registration numbers will be reported by Dr. Jell (information not available)]

Table 5.—Set I data. Location of the madreporite in specimens that obey Lovén's law.

I/II	II/III	III/IV	IV/V	V/I
0	0	12	0	0

Set II: Nineteen specimens. Details are as follows (specimen numbers according to Table 5):

201. *Encrinaster hamlingi* Spencer, holotype, Institute of Geological Sciences, Leeds, Nos. GSM 37360, GSM 37361, Lower Carboniferous, Croyde, North Devon (counterpart halves; seen) (Hotchkiss 1978: specimen no. 2)

202. *Taeniaster spinosus* (Billings), holotype of *Protaster? granuliferus* Meek, Museum of Comparative Zoology, Harvard University, No. MCZ 470, Richmond Group (Middle Ordovician), Moore's Hill, Indiana (oral view; studied from the photograph: Hotchkiss 1970:fig. 6) (Hotchkiss 1978:specimen no. 13)

203. *Stratаster ohioensis* Kesling & LeVasseur, paratype L-25e, Meadville Shale (Early Missippian), Cuyahoga County, Ohio (oral view; studied from the photograph: Kesling & LeVasseur 1971:pl. 4 fig. 1; pl. 10, fig. 4) (Hotchkiss 1993:65)

204. *Stratаster ohioensis* Kesling & LeVasseur, paratype L-25i, Meadville Shale (Early Missippian), Cuyahoga County, Ohio (oral view; studied from the photograph: Kesling & LeVasseur 1971:pl. 6 fig. 2) (Hotchkiss 1993:65)

205. *Stratаster maciverorum* Hotchkiss, topotype, Panther Mountain Formation (Middle Devonian), near Cooperstown, New York; New York State Museum (uncatalogued McIver collection: rock specimen DS12) (oral view; seen) (McIver & McIver 1955, Hotchkiss 1993:73)

206. *Stratаster maciverorum* Hotchkiss, topotype, Panther Mountain Formation (Middle Devonian), near Cooperstown, New York; New York State Museum (uncatalogued McIver collection: rock specimen DS70) (oral view; seen) (McIver & McIver 1955, Hotchkiss 1993:73)

207. *Taeniaster spinosus* (Billings), holotype of *T. schohariae* Ruedemann, New York State Museum No. 7784, Schenectady beds (Middle Ordovician), near Schoharie Junction, New York. (oral view; seen) (Kilfoyle 1954:204, 639; Hotchkiss 1970:fig. 3).

208. *Protasterina fimbriata* Ulrich, holotype, Economy Formation (Middle Ordovician), Covington, Kentucky, University of Cincinnati Geology Museum No. 25001 (oral view; seen) (Schuchert 1915:pl. 36 fig. 4) (Hansman et al. 1962)

209. *Protasterina fimbriata* Ulrich, Utica Slate, Cincinnati, Ohio, American Museum of Natural History

AMNH 13190 (labeled *Protaster flexuosa* Miller & Dyer; Faber exchange) (oral view; seen; madreporite partly covered by spines)

210. *Eugasterella logani* (Hall), Moscow Formation (Middle Devonian), near Earlville, Madison County, New York, photograph published by Harper (1985:fig. 2B, fig. 3), Carnegie Museum of Natural History No. CM 34421A (oral view; studied from the photograph)

211. *Protaster whiteavesianus* Parks, syntype, Middle Ordovician Trenton Group, Kirkfield, Ontario. Royal Ontario Museum No. 23846, inked #638T specimen B (oral view; fragmentary; seen) (Parks 1908:368, Waddington et al. 1978:132).

212. *Taeniaster ibericus* Hammann & Schmincke, holotype, Museum of the Instituto Geológico y Minéro, Madrid, No. S 587/2, "*Tristani*-beds" (Middle Ordovician), near Fontanosas, Spain (oral view; studied from the photograph: Hammann & Schmincke 1986:fig. 8d.)

213. *Taeniaster ibericus* Hammann & Schmincke, paratype, Museum of the Instituto Geológico y Minéro, Madrid, No. S 587/1, "*Tristani*-beds" (Middle Ordovician), near Fontanosas, Spain (oral view; studied from the photograph: Hammann & Schmincke 1986: fig. 10.)

214. *Taeniaster ibericus* Hammann & Schmincke, paratype, Museum of the Instituto Geológico y Minéro, Madrid, No. S 587/5, "*Tristani*-beds" (Middle Ordovician), near Fontanosas, Spain (oral view; studied from the photograph: Hammann & Schmincke 1986: fig. 7a, 7c.)

215–219. Protasteridae sp., Devonian Bokkeveld Group, South Africa. [oral views; studied from photographs loaned by Dr. P. A. Jell; material is under study by Dr. Jell; repository and registration numbers will be reported by Dr. Jell (information not available)]

Excluded: The following excluded specimens deserve special comment. For convenience of future reference they are numbered:

301. *Armathyraster paradoxis* Harper & Morris, Brush Creek Shale (Pennsylvanian), Punxsutawney, Jefferson County, Pennsylvania, ABA*AA arrangement described by Harper & Morris (1978:157) [Carnegie Museum of Natural History No. CM 33966; counterpart halves; the aboral view is easily scored.] Excluded because the location of the madreporite is doubtful: it is "not well enough preserved for complete identification" (Harper & Morris 1978:157). The reported score ABA*AA contains three disparities with the expected AAB*AB. An alternative possibility is that the hydropore is not associated with a visible madreporite, and that the specimen scores as AAB(*?)AA or AAA(*?)AB with only one disparity.

302. *Bohemura jahni* Jaekel, figured specimen, Letna Formation, Haj near Zahorany. National Museum [Narodni Museum], Prague, No. NM L 10172. Excluded because none of the arms are scorable; in the published drawing (Petr 1988:fig. 1a) details of ambs around the mouth opening were filled in for the purpose of illustration. (Oral view; latex pull supplied by Dr. Petr)

303. *Bohemura jahni* Jaekel, lectotype, Zahorany Formation, Zahorany near Beroun. National Museum [Narodni Museum], Prague, No. NM L 10066 [formerly registered as No. EH 146]. Excluded because none of the arms are scorable; the drawing published by Spencer (1934:473, text-fig. 305; reproduced in Spencer & Wright 1966:U86 fig. 75,2a) was found by Petr (1989:1) to be incorrect. This specimen was reillustrated by Petr (1989:6, text-fig. 2, pl. I) and was designated the lectotype. (Oral view; latex pull supplied by Dr. Petr)

304. *Euzonosoma orbitoides* Spencer, holotype, Thraive Glen Starfish Bed. British Museum (Natural History) No. BMNH E52424b [formerly No. D. 52c in Mrs. Gray's colln.] (Owen 1965:552, Lewis 1993: 69). Excluded because the location of the madreporite is doubtful: it is not distinct enough from the other disc plates for certain identification in this specimen. The detail of amb IV in the drawing published by Spencer (1930:414, text-fig. 265, indicating the amb arrangement ???*B?; drawing reproduced in Spencer & Wright 1966:U85 fig. 74,4b) is not confirmed by the fossil. I score the fossil as AA?(*?)A?. (Oral view; latex pull supplied by D. N. Lewis)

305. *Protaster piltonensis* Spencer, holotype, Lower Carboniferous of Top Orchard Quarry, Pilton, Devon. British Museum (Natural History) No. BMNH E13835b [formerly No. 1292 in the Torquay Natural History Society Collection] (Owen 1965:549, Lewis 1993:75). Excluded because none of the arms are scorable. The detail of amb IV in the drawing published by Spencer (1934:470, text-fig. 304, indicating the amb arrangement ???*B?) is not present in the fossil. (Oral view; latex pull supplied by D. N. Lewis)

Results and analysis of Set I data.—The plate arrangements of the twelve Lovénian specimens are used to label the arms as I, II, III, IV, V. The madreporite is found only in interradius III/IV (Table 5). Under the null hypothesis of no preferred placement of the madreporite, the probability of observing the madreporite in the same interradius (not specifically the III/IV interradius, but any interradius) in all twelve specimens is

$$(0.2)^{11} = 0.00000002$$

Therefore the null hypothesis is rejected. The madreporite occurs in interradius III/IV more frequently than can be accounted for by chance alone.

Results and analysis of Set II data.—The madreporite is used to label interradius III/IV. The remaining arms are labeled according to their placement with respect to the madreporite. This before-the-fact label-

Table 6.—Set II data. The madreporite is used as a landmark to label the arms I, II, III, IV, V. The A or B score of each scorable arm is recorded in the table.

	Specimen	I	II	III	*	IV	V
201	*Encrinaster hamlingi*	—	B	B	*	A	A
202	*Taeniaster spinosus*	—	B	B	*	A	—
203	*Strataster ohioensis*	A	—	B	*	A	B
204	*Strataster ohioensis*	—	A	—	*	—	—
205	*Strataster maciverorum*	A	A	—	*	A	B
206	*Strataster maciverorum*	—	—	B	*	—	—
207	*Taeniaster spinosus*	—	—	B	*	—	—
208	*Protasterina fimbriata*	A	A	—	*	A	B
209	*Protasterina fimbriata*	A	B	—	*	B	A
210	*Eugasterella logani*	A	A	B	*	A	—
211	*Protaster whiteavesianus*	—	—	B	*	—	—
212	*Taeniaster ibericus*	—	—	—	*	A	—
213	*Taeniaster ibericus*	—	—	—	*	—	B
214	*Taeniaster ibericus*	A	A	B	*	—	—
215	Protasteridae sp.	—	A	B	*	A	—
216	Protasteridae sp.	A	A	—	*	A	B
217	Protasteridae sp.	A	A	B	*	—	—
218	Protasteridae sp.	—	A	B	*	—	B
219	Protasteridae sp.	A	A	B	*	A	—

ing is based on having a working hypothesis and provides the convenience of not having to relabel the arms after doing the analysis. The A or B score of each arm is entered in Table 6. The working hypothesis is that the arms have predominant character states, these states spell out Lovén's law, and ray numbering based on Lovén's law places the madreporite in interradius III/IV.

The data of Table 6 are summarized in Table 7. The predominant character states occur more frequently than can be accounted for by chance alone (one sided test; see Note 14). It is seen that the predominant character states of the arms spell out Lovén's law. Numbering the rays based on recognizing Lovén's law shows that the madreporite occurs in interradius III/IV.

Table 7.—Analysis of Set II data. The working hypothesis is that the observed character states will spell out Lovén's law in a way that places the madreporite in interradius III/IV. Table entries record the number of times that the working hypothesis is fulfilled and the probability (*P*) of observing this many or more of the stated character under the null hypothesis HO of chance alone.

Arm I has arrangement A in 9 out of 9 specimens, $P = 0.00195$
Arm II has arrangement A in 10 out of 13 specimens, $P = 0.0461$
Arm III has arrangement B in 12 out of 12 specimens, $P = 0.000244$
Arm IV has arrangement A in 10 out of 11 specimens, $P = 0.00586$
Arm V has arrangement B in 6 out of 8 specimens, $P = 0.145$
Lovénian arrangement found in 47 out of 53 arms